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The brain basis of emotion: A meta-analytic review

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Abstract: Researchers have wondered how the brain creates emotions since the early days of psychological science. With a surge of studies in affective neuroscience in recent decades, scientists are poised to answer this question. In this target article, we present a meta-analytic summary of the neuroimaging literature on human emotion. We compare the locationist approach (i.e., the hypothesis that discrete emotion categories consistently and specifically correspond to distinct brain regions) with the psychological constructionist approach (i.e., the hypothesis that discrete emotion categories are constructed of more general brain networks not specific to those categories) to better understand the brain basis of emotion. We review both locationist and psychological constructionist hypotheses of brain–emotion correspondence and report meta-analytic findings bearing on these hypotheses. Overall, we found little evidence that discrete emotion categories can be consistently and specifically localized to distinct brain regions. Instead, we found evidence that is consistent with a psychological constructionist approach to the mind: A set of interacting brain regions commonly involved in basic psychological operations of both an emotional and non-emotional nature are active during emotion experience and perception across a range of discrete emotion categories.

Keywords: Discrete emotion; emotion experience; emotion perception; meta-analysis; neuroimaging; psychological construction

1. Introduction

William James framed the question of emotion–brain correspondence when he wrote, "of two things concerning the emotions, one must be true. Either separate and special centres, affected to them alone, are their brain-seat, or else they correspond to processes occurring in the motor and sensory centres already assigned" (James 1890/1998, p. 473). In this target article, we statistically summarize the last 15 years of neuroimaging research on emotion in an attempt to determine which of these alternatives is correct. We examine the utility of two different models of emotion that have each existed since the beginning of psychology.

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2. A locationist account of the brain basis of emotion

A *locationist* account of emotion assumes that the category *emotion* and individual categories such as *anger*, *disgust*, *fear*, *happiness*, *sadness* (and perhaps a few others) are respected by the body and brain (see Barrett [2006a] for a discussion). The guiding hypothesis of this natural kind model (Barrett 2006a) or modal model (Barrett et al. 2007d) of emotion is that different emotion categories refer to states with endowed motivational characteristics that drive cognition and behavior. It is assumed that these states are biologically basic and inherited, and cannot be broken down into more basic psychological components (Ekman & Cordaro 2011; Izard 2011; Panksepp & Watt 2011). Despite these common assumptions, there is variability in how different researchers define emotions as natural kinds. Some theorists emphasize the universal characteristics of emotion categories, suggesting that each emotion category (e.g., *anger*) refers to a "family" of states that share a distinctive universal signal (e.g., facial behavior), physiology, antecedent events, subjective experience, and accompanying thoughts and memories (e.g., Ekman & Cordaro 2011). In this view, emotions can be shaped by culture and learning, but all humans possess the capacity to experience and perceive the same core set of emotion categories.

Other theorists take a developmental approach and argue that all infants are born with a set of "first order emotions" that are evolutionarily given reactions (including feelings, motivations and behaviors) to specific stimuli (e.g., Izard 2011). First order emotions form the core of the more elaborate "emotion schemas" that develop with age and learning and consist of complex combinations of emotions, cognitions, and behaviors. Still other theorists emphasize the evolutionary aspect of emotion categories, and argue that emotions are specific behavioral adaptations that are shared with other mammalian species and passed down through phylogeny (e.g., Panksepp 1998; 2007; Panksepp & Watt 2011). Some models taking an "appraisal" approach to emotion also draw on natural kind assumptions about emotions (cf. Barrett 2006a) by hypothesizing that dedicated cognitive mechanisms automatically make meaning of a stimulus and trigger the corresponding discrete emotion (e.g., Roseman 1984; Ellsworth & Scherer 2003). Relatively little work from an appraisal perspective has investigated the brain basis of emotion (although see Sander et al. 2003; 2007). Therefore, we do not discuss appraisal models further in this article.

All natural kind models share the assumption that different emotion categories have their roots in distinct mechanisms in the brain and body. The mechanisms underlying discrete emotion categories have been discussed as residing within particular gross anatomical locations (e.g., Calder 2003; Ekman 1999) or networks (e.g., Izard 2011; Panksepp 1998) in the brain. These models constitute a locationist account of emotion because they hypothesize that all mental states belonging to the same emotion category (e.g., *fear*) are produced by activity that is consistently and specifically associated with an architecturally defined brain locale (see sections 5.1–5.4 further on)[1] or anatomically defined networks of locales that are inherited

and shared with other mammalian species (Panksepp 1998; Panksepp & Watt 2011). Not all natural kind models are locationist, however; for example, some models propose that each discrete emotion is triggered by an inherited mechanism (e.g., an "affect program"; Ekman & Cordaro 2011; Tomkins 1962; 1963) that does not necessarily correspond to a particular brain locale but rather to a specific pattern of autonomic nervous system activity. Much of the contemporary research on emotion makes locationist assumptions; in this article we focus on the models that hypothesize single brain regions to be consistently and specifically associated with different emotion categories, because they represent the most frequent hypothesis that has been tested in the cognitive neuroscience literature. We discuss specific predictions of the locationist approach in section 5, Testing Hypotheses of Brain–Emotion Correspondence (also see Fig. 1).

3. A psychological constructionist account of the brain basis of emotion

A *psychological constructionist* account of emotion assumes that emotions are psychological events that emerge out of more basic psychological operations that are not specific to emotion. In this view, mental categories such as *anger, sadness, fear*, et cetera, are not respected by the brain (nor are *emotion*, *perception*, or *cognition*, for that matter; Barrett 2009a; Duncan & Barrett 2007; Pessoa 2008). A psychological constructionist approach to emotion is as old as the locationist approach, at least in its nascent form (e.g., Wundt, James, and other early psychologists were psychological constructionists; see Gendron & Barrett 2009). Our contemporary psychological constructionist approach shares much in common with cognitive neuroscience approaches arguing that basic psychological operations are common across diverse task domains (Cole & Schneider 2007; Dosenbach et al. 2006; Smith et al. 2009; van Snellenberg & Wager 2009; Wager et al. 2005; Wager & Smith 2003). As in the neural context hypothesis, it assumes that the psychological function of individual brain regions is determined, in part, by the network of brain regions it is firing with (McIntosh 2004). It is also consistent with recent evidence that large-scale networks intrinsic to the brain interact to produce psychological events (Seeley et al. 2007; Smith et al. 2009; Spreng et al. 2009; see Deco et al. [2011] for a review). In philosophy of mind, it is consistent with both a token identity and a supervenience approach to mind–brain correspondence (Barrett 2011) and the mental mechanisms approach (Bechtel 2008). We discuss the psychological constructionist view in a bit more detail because it is unfamiliar to many readers.

In our psychological constructionist model, called the "conceptual act model," emotions emerge when people make meaning out of sensory input from the body and from the world using knowledge of prior experiences. Emotions are "situated conceptualizations" (cf. Barsalou 2003) because the emerging meaning is tailored to the immediate environment and prepares the person to respond to sensory input in a way that is tailored to the situation (Barrett 2006b). "Conceptual acts" could also be called "perceptual acts" because they are thought to emerge in consciousness just as visual and auditory percepts do when sensory input is automatically and effortlessly made meaningful using knowledge from prior experience. The idea is that the brain makes an initial prediction about the meaning of the sensory array in context (Bar 2007), and the error between this initial top-down prediction and the sensory activity is quickly minimized (Friston 2010) to produce a unified conscious field.

In psychological construction, all mental states, whether they are experienced as an instance of a discrete emotion category or not, are realized by more basic psychological

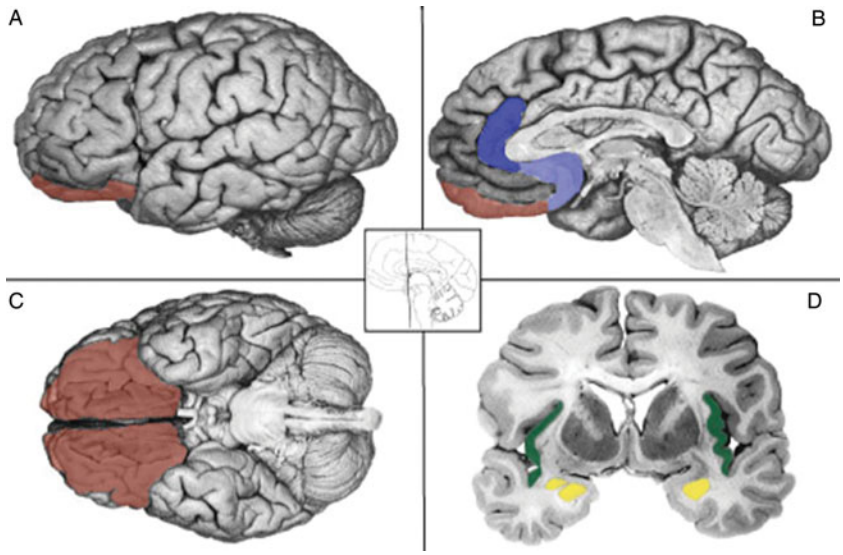

Figure 1. Locationist Hypotheses of Brain–Emotion Correspondence. A: Lateral view. B: Sagital view at the midline. C: Ventral view. D: Coronal view. Brain regions hypothesized to be associated with emotion categories are depicted. Here we depict the most popular locationist hypotheses, although other locationist hypotheses of brain–emotion correspondence exist (e.g., Panksepp, 1998).

Fear: amygdala (yellow); *Disgust:* insula (green); *Anger:* OFC (rust); *Sadness:* ACC (blue). A color version of this image can be viewed in the online version of this target article at http://www.journals.cambridge.org/bbs.

operations or "ingredients" of the mind. The goal of psychology is to identify these psychological operations as "psychological primitives," or the most basic psychological descriptions that cannot be further reduced to anything else mental (because at that point they would describe biological mechanisms). These basic psychological operations are not functionally specific to any discrete emotion category, or even to the category *emotion* itself. Instead, they are functionally selective for emotion on certain occasions. Because our own model is relatively new, our current model has not identified the most primitive level of psychological description, and it is not yet possible to definitively claim what the most basic psychological operations of the mind are. What we propose is a set of basic domains of psychological function that are a first approximation in the trajectory of a longer research program to identify psychological primitives. These will no doubt be refined as research proceeds in the coming years.

One operation in all psychological constructionist models of emotion is some form of sensory input from the body, such as raw somatic, visceral, vascular, and motor cues (James 1884), arousal (Duffy 1957; Mandler 1975; 1990; Schachter & Singer 1962), or affect (Harlow & Stagner 1932; Hunt 1941; Wundt 1897/1998). In our psychological constructionist view, we refer to this basic psychological domain, as "core affect" (Barrett 2006b; Barrett & Bliss-Moreau 2009; Russell 2003; Russell & Barrett 1999). In psychology, the word "affect" is used to mean anything that is emotional. Core affect, on the other hand, is a term used to describe the mental representation of bodily changes that are sometimes experienced as feelings of hedonic pleasure and displeasure with some degree of arousal (Barrett & Bliss-Moreau 2009; Russell 2003; Russell & Barrett 1999). Core affect is realized, in part, by visceral control systems that help organisms deal with motivationally salient stimuli in the environment. A functioning peripheral nervous system is not necessary for a person to experience a core affective state (e.g., Critchley et al. 2001) as long as they have some prior experiences to provide them with central nervous system representations of bodily states. However, in healthy individuals, core affect is usually accompanied by somatovisceral, kinesthetic, proprioceptive, and neurochemical fluctuations that take place within the core of the body and are represented in the brain. Changes in core affect are a homeostatic barometer – the body's way of representing whether objects in the environment are valuable or not in a given context. The concept of core affect shares much in common with the idea that bodily cues constitute a core ingredient in mental life (e.g., the idea that being embodied is essential to consciousness: Craig 2009; Damasio 1999; the idea that feelings are a common currency for valuation of objects in the world: Cabanac 2002). We assume that core affect is not psychologically meaningful unless it is attached to an object; it is made meaningful via a second basic psychological operation, which we describe next.

All psychological constructionist models include a second basic psychological operation by which internal sensory cues or their associated affective feelings are automatically and effortlessly made meaningful (i.e., experienced as related to or caused by an event or object, usually in the external surroundings). Candidates for this second psychological operation include ideas (Wundt 1897/1998), social affiliation (Schachter & Singer 1962), attribution (Russell 2003), or, as we propose in our model, categorization as situated conceptualization (Barrett 2006b). The process of "conceptualization" (and the other operations that support it, such as executive attention) links perceptions of sensory input from the world with input from the body to create a meaningful psychological moment. In our hypothesis, people automatically make meaning of their core affective state by engaging in a situated conceptualization that links it to an object or event. Conceptualization is the process by which stored representations of prior experiences (i.e., memories, knowledge) are used to make meaning out of sensations in the moment (Wilson-Mendenhall et al. 2011). A person can make the situated conceptualization that core affect is a physical symptom (e.g., a racing heart), a simple feeling (e.g., feeling tired or wound up), or an instance of a discrete emotion category (e.g., *anger* vs. *fear*). And at other times, core affect is perceived as part of an object itself rather than one's reaction to it. For instance, a food is delicious or distasteful, a painting is beautiful or garish, or a person is nice or nasty. Because we hypothesize that people make meaning of their core affective states in context, experiencing them as a part of an emotion, perception, belief, or judgment, a psychological constructionist account does not simply reduce the category of *emotion* to positive or negative affect (as is often claimed in summaries of "dimensional models of emotion"; e.g., Fontaine et al. 2007; Keltner et al. 2003). Conceptualization can be said to produce cognitive appraisals realizing emotion (Barrett et al. 2007c), where such appraisals are descriptions of the features or properties of emotional experience (Clore & Ortony 2008). In many appraisal models, the assumption is that the brain contains a series of specific cognitive appraisal mechanisms (e.g., there is a specific mechanism to appraise the novelty of an object, or whether one's goals are blocked) which, when configured into a particular pattern, trigger discrete emotions. In our model, we do not propose any new or unique mental processes that cause emotion; instead, we propose a mechanism (categorization) that has been well documented in the psychological and cognitive neuroscience literature. Categorization (or conceptualization) is a fundamental process in the human brain that functions like a chisel, leading people to attend to certain features in a sensory array and to ignore others. Only some of the wavelengths of light striking our retinas are transformed into seen objects, only some of the changes in air pressure registered in our ears are heard as words or music, and only some bodily changes are experienced as emotion. To categorize something is to render it meaningful. It then becomes possible to make reasonable inferences about that thing, to predict what to do with it, and to communicate our experience of it to others. There are ongoing debates about how categorization works, but the fact that it works is not in question.

In our model, categorization in the form of situated conceptualization is realized in a set of brain regions that reconstitutes prior experiences for use in the present. This set of brain regions has also been called the "episodic memory network" (e.g., Vincent et al. 2006) or the "default network" (e.g., Raichle et al. 2001). It is active when people recall the past (e.g., Buckner & Carroll 2007; Schacter et al. 2007; see also, McDermott et al. [2009] for a meta-analysis), imagine the future (e.g., Addis et al. 2007; see also, Hassabis & Maguire 2009; Moulton & Kosslyn 2009; Schacter et al. 2007), make context-sensitive

Definitions

Natural kind approach. A theoretical framework for understanding the ontology of emotions. The natural kinds approach assumes that emotion categories such as *anger*, *sadness*, *fear*, et cetera, map on to biological categories that are given by the brain and body, and cannot be reduced to more basic psychological parts.

Locationist approach. Many national kind models of emotion conform to a locationist approach in which discrete emotion categories (e.g., *anger*) are assumed to be consistently and specifically localized to discrete brain locales or anatomical networks.

Psychological constructionist approach. A theoretical framework for understanding the ontology of emotions. The psychological constructionist approach assumes that emotion categories such as *anger*, *sadness*, *fear*, and so forth, are common sense categories whose instances emerge from the combination of more basic psychological operations that are the common ingredients of all mental states.

Core affect. The mental representation of bodily sensations that are sometimes (but not always) experienced as feelings of hedonic pleasure and displeasure with some degree of arousal. Core affect is what allows an organism to know if something in the environment has motivational salience (i.e., is good for it, bad for it, approachable, or avoidable). Barring organic abnormality, core affect is accompanied by somatovisceral, kinesthetic, proprioceptive, and neurochemical fluctuations that take place within the core of body and feed back to be represented in the brain.

Conceptualization. The process by which sensations from the body or external world are made meaningful in a given context using representations of prior experience. Conceptualization occurs in a situated fashion (as in "situated conceptualization"; see Barsalou 2003), drawing on the representations of prior experience that are activated by the present physical and psychological situation.

Executive attention. The process by which some representations are selectively enhanced and others are suppressed. This is also known as "endogenous," "controlled," or "goal-based" attention and can be exerted both volitionally and without the conscious experience of volition. Executive attention can shape the activity in other processes such as core affect, conceptualization, or language use. In the case of emotion, executive attention foregrounds certain core affective feelings and exteroceptive sensory sensations in a moment, and guides which situated conceptualizations are brought to bear to make meaning of those sensations in the given context.

Emotion words. The set of words that ground the abstract categories that humans experience and communicate about. In the case of abstract categories like emotions, words are "essence placeholders" that help cohere feelings, behaviors, and facial expressions together as instances of a meaningful category.

Neural reference space. The set of neurons that are probabilistically involved in realizing a class of mental events (such as *anger*, or even *emotion*).

Functional selectivity. This occurs when a set of neurons show a consistent increase in activation for one mental state (e.g., *anger*, *disgust*, *emotion*) or basic psychological operation (e.g., categorization, core affect) more so than for others in a given instant. The neurons are not specific to any mental state, although they might be more frequently activated in some than in others. Functional selectivity might occur because a brain region supports a more basic psychological operation that helps to construct a certain mental state (e.g., the amygdala supports detection of salient exteroceptive sensations and is functionally selective for perceptions of *fear*). A brain area might be functionally selective for one mental state or even one basic psychological operation in one instance, and for another state or operation in another instance (e.g., ventromedial prefrontal cortex helps to realize both core affect and conceptualization).

predictions about others' thoughts and feelings (e.g., as in theory of mind; Saxe & Kanwisher 2003; see Mitchell 2009), or make meaning of exteroceptive sensations (e.g., context-sensitive visual perception; Bar et al. 2006; see also, Bar 2009). In emotion, we hypothesize that this psychological operation makes a prediction about what caused core affective changes within one's own body or what caused the affective cues (e.g., facial actions, body postures, or vocal acoustics) in another person, and this prediction occurs in a context-sensitive way (with the result that core affect in context is categorized as an instance of *anger*, *disgust*, *fear*, etc.; Barrett 2006b; 2009b; see also, e.g., Barrett & Kensinger 2010; Lindquist & Barrett 2008a; Wilson-Mendenhall et al. 2011). When making meaning out of core affect, conceptualization draws on prior experiences and perceptions of emotion to realize the emotional gestalts that make up part of what Edelman calls "the remembered present" (cf. Edelman 1989; see Barrett et al. 2007c; Barrett 2009b).

Our model proposes two additional operations that are important to the psychological construction of emotion. We hypothesize that emotion words that anchor emotion categories work hand in hand with conceptualization (Barrett 2006b; Barrett et al. 2007b). Emotion words are essential to our model because we assume that the instances of any emotion category (e.g., *anger*) that are created from affective feelings don't have strong statistical regularities in the real world or firm natural category boundaries (for a discussion of the empirical evidence, see Barrett 2006a; 2009; Barrett et al. 2007a). In our view, emotion categories are abstract categories that are socially constructed (Barrett 2009a). As with all abstract categories, in the absence of strong perceptual statistical regularities within a category, humans use words as the glue that holds the category together (Barsalou & Weimer-Hastings 2005). In fact, even infants routinely use the phonological form of words to make conceptual inferences about novel objects that share little perceptual

similarity (Dewar & Xu 2009; Ferry et al. 2010; Xu 2002), and we believe that adults do the same thing. Because words are in part represented via situated simulations of prior experiences (e.g., Simmons et al. 2008), we expect emotion words to work together with conceptualization when perceivers make meaning of core affective states.

Executive attention is the fourth operation that is particular to our psychological constructionist approach (Barrett 2009a; Barrett et al. 2004). Executive attention helps direct the combination of other psychological operations to produce an emotional gestalt. At any point in time, the brain is processing information from the body (core affect), information from outside the body (exteroceptive sensory information), and representations of prior experiences (conceptualizations). For instance, many different representations of the past might become active to make meaning of a core affective state. We hypothesize that executive attention helps determine which representations are utilized to make meaning of that state, and which are suppressed (cf. Barrett 2009b; see Barrett et al. 2004, for a discussion). Executive attention can also control which exteroceptive sensory representations are favored for additional processing, or if core affect is consciously represented in awareness. Importantly, executive attention need not be volitional or effortful and can operate well before subjective experience is generated (Barrett et al. 2004). We acknowledge that additional operations are probably important to the construction of emotion and will be incorporated into our model as research accrues.

In the past, most researchers who found brain correlates of emotion assumed that their results were consistent with a locationist approach (e.g., the basic emotion approach) because these were the only models to map psychological states to a biological level of analysis in a way that was linked to evolution. Constructionist hypotheses (which were typically social, rather than psychological) were restricted to the psychological level in a manner divorced from evolution. But this is an accident of history. In fact, there are very clear brain hypotheses that develop from a psychological constructionist view (Barrett 2006b), and our psychological constructionist approach is the first that attempts to map basic psychological operations to brain networks that comprise instances of a psychological category such as *emotion*, or to the subordinate categories of *anger*, *sadness*, *fear*, *disgust*, and *happiness* (see also Barrett 2006a; 2006b; 2009a; 2009b; Barrett et al. 2007a; 2007c; Kober et al. 2008). Our hypothesized psychological operations, as they currently stand, are associated with assemblies of neurons within distributed networks (rather than a one-to-one mapping of ingredient to network). We hypothesize that these networks combine and constrain one another like ingredients in a recipe, influencing and shaping one another in real time according to the principles of constraint satisfaction (Barrett et al. 2007d). With more research, it will be possible to identify the distributed brain networks that are associated with the most basic psychological operations of the mind.

Together, the functional networks that instantiate basic psychological operations during emotion experiences and perceptions form the "neural reference space for discrete emotion." According to Gerald Edelman (1989), a "neural reference space" is made up of the neurons that are probabilistically involved in realizing a class of mental events (such as *anger*, or even *emotion*).[2] The functions of distinct brain areas within the neural reference space are best understood within the context of the other brain areas to which they are connected (either anatomically or because of the timing and coordination of neural activity) and in terms of the basic psychological operations they are functionally selective for in a given instance. Unlike a locationist approach, which hypothesizes that a single brain region will be consistently and specifically activated across instances of a single emotion category, a psychological constructionist approach hypothesizes that the same brain areas will be consistently activated across the instances from a range of emotion categories (and, although it is beyond the scope of this article, even in non-emotional states), meaning that that brain region is not specific to any emotion category (or even to *emotion* per se). We focus on the brain regions that we believe are hubs in the networks corresponding to basic psychological operations and discuss specific predictions in section 5, "Testing Hypotheses of Brain–Emotion Correspondence" (also see Fig. 2).

4. Meta-analysis of neuroimaging studies on emotion

In this article, we report a meta-analysis of neuroimaging studies on emotion to assess whether the data are more consistent with a locationist or a psychological constructionist account of emotion. In our meta-analysis, strong evidence for a locationist account would be found if instances of an emotion category (e.g., *fear*) are *consistently* and *specifically* associated with increased activity in a brain region (or a set of regions within an anatomically inspired network) across published neuroimaging studies. *Consistency* refers to the fact that a brain region shows increased activity for every instance of an emotion category (e.g., the amygdala shows increased activity each time a person experiences an instance of the category *fear*). *Specificity* refers to the fact that a given brain region is active for instances of one (and only one) emotion category (e.g., the amygdala does not show increased activity when a person is experiencing an instance of *anger*, *disgust*, *happiness*, or *sadness*). Support for a psychological constructionist view, in contrast, would be found if the same brain region(s) were involved in realizing instances of several emotion categories – and, furthermore, if the brain region(s) are more generally important to realizing a basic psychological operation (e.g., core affect, conceptualization, language, or executive attention). From this perspective, we would not expect instances of any emotion category to be specifically related to increased activation in any single brain region or set of regions. A brain region might be functionally selective for a given emotion category in a given instance, however, because it helps realize a more basic operation that contributes to the emergent state.

In 2005, we began our meta-analytic project to probe the brain basis of emotion. We have since published one chapter (Wager et al. 2008) and two papers (Barrett et al. 2007c; Kober et al. 2008) reporting our findings for the neuroimaging studies of discrete emotion and affect that came out between 1990 and 2005. Supporting a psychological constructionist approach to emotion, we found that the neural reference space for emotion and affect could be inductively parsed into six distributed

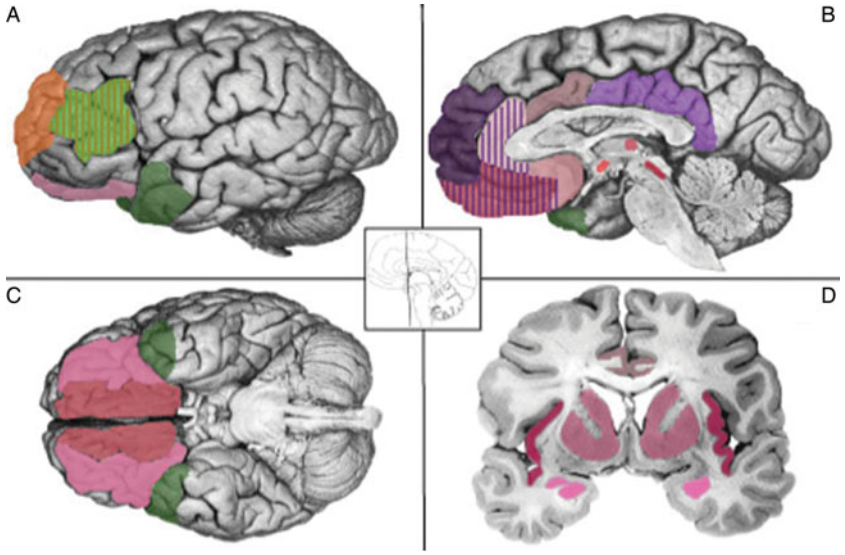

Figure 2. Psychological Constructionist Hypotheses of Brain–Emotion Correspondence. A: Lateral view. B: Sagital view at the midline. C: Ventral view. D: Coronal view.

Brain regions hypothesized to be associated with psychological operations are depicted. In some cases, we present only the key brain regions within networks that have been empirically linked to our hypothesized psychological operations. In instances where the whole brain network is not depicted, we point readers to relevant literature.

Core Affect (pink): amygdala, insula, mOFC (Bas 10m, 11m, 13a, b, 14r, c), lOFC (BAs 47, 12, 13l, m, 11l), ACC (Bas, 32, 24, 25), thalamus, hypothalamus, bed nucleus of the stria terminalis, basal forebrain, PAG. *Conceptualization* (purple): VMPFC (Bas 11, 25, 32, 34), DMPFC (BAs 9, 10p), medial temporal lobe* (hippocampus, entorhinal cortex, parahippocampal cortex), posterior cingulate cortex/retrosplenial area (BA 23, 31). *Language* (green): VLPFC (Bas 44, 45, 46), anterior temporal lobe (BA 38); for additional regions, see Vigneau et al. (2006). *Executive Attention* (orange): DLPFC (BAs 9, 10, 46), VLPFC (BAs 44, 45, 46); for additional regions see Corbetta & Shulman, (2002); Dosenbach et al. (2006); Wager et al. (2004). (*this structure is not visible in this view of the brain). A color version of this image can be viewed in the online version of this target article at http://www.journals.cambridge.org/bbs.

functional groups of brain regions (i.e., regions consistently co-activated across studies) using a series of multidimensional scaling and cluster analyses (Kober et al. 2008) (See Fig. 3). These functional groups can be mapped to the hypothesized psychological operations that we derived from behavioral data (e.g., Barrett 2006).

4.1. Analysis strategy

In the present article, we expanded upon our initial meta-analytic efforts to directly compare the locationist versus the psychological constructionist approach for neuroimaging studies of discrete emotion. A detailed description of our meta-analytic methods and Figure S1 are included in the supplementary materials (available at: http://www.journals.cambridge.org/bbs2012008). In comparing these hypotheses, we are comparing a hypothesis with very specific empirical requirements (i.e., evidence for consistency and specificity in brain–emotion correspondence) to a hypothesis with more flexible empirical requirements (i.e., evidence of multiple operations across multiple categories). Given the popularity of

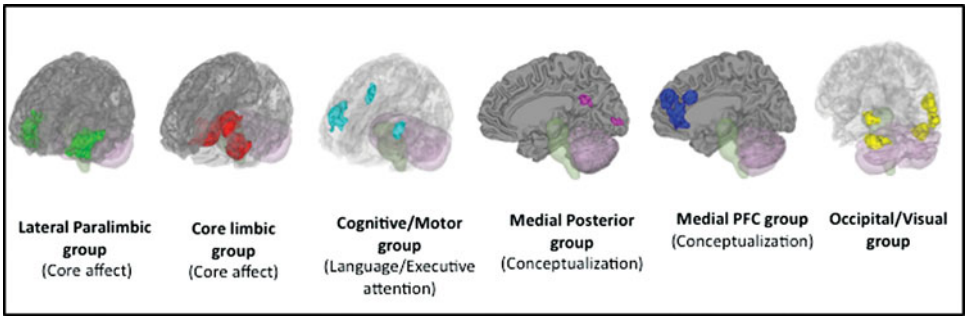

Figure 3. Kober et al.'s (2008) Functional Clusters. Kober et al.'s (2008) six functional clusters are consistent with the ingredients hypothesized by our psychological constructionist model. The brain areas making up the "core limbic group" and "lateral paralimbic group" are part of the network that helps to constitute core affect. Aspects of the "medial posterior group" and "medial PFC group" are part of the network involved with conceptualization. Areas in the "cognitive/motor control group" are consistent with the networks supporting language and executive attention. In addition, an "occipital/visual group" was also identified as part of the neural reference space for emotion. Visual cortex has connectivity with areas involved in core affect (e.g., amygdala, orbitofrontal cortex; Amaral & Price 1984; Barrett & Bar 2009; Pessoa & Adolphs 2010), and there is growing evidence that a person's core affective state modulates activity in primary visual cortex (Damaraju et al. 2009). Core affect even shapes aspects of visual perception ranging from contrast sensitivity (Phelps et al. 2006) to visual awareness (Anderson et al. 2011). A color version of this image can be viewed in the online version of this target article at http://www.journals.cambridge.org/bbs.

locationist models of emotion, we made analysis choices that favored a clear and unbiased test of the locationist approach, even though it disadvantaged us in testing the full scope and power of the psychological constructionist approach. After updating our database to include papers from 2006 and 2007, we exclusively sampled studies that focused on discrete emotion experiences or perceptions to increase the likelihood that we would find consistent and specific brain localizations corresponding to these categories, should they exist (see Tables S1 and S2 in supplementary materials for details on the inclusion criteria and database; available at: http://www.journals.cambridge.org/bbs2012008). We also conducted a number of statistical analyses with the potential to yield evidence in favor of a locationist account (outlined in the next section).

4.1.1. The neural reference space for discrete emotion. We began by estimating the neural reference space for discrete emotion. This space refers to the brain regions that show a consistent increase in activation for the experience or perception of instances of *anger, sadness, fear, disgust*, and *happiness*. A brain region might appear in this space because its activation consistently increases in studies of one discrete emotion category but not others, some categories but not others, or all categories of emotion. Alternatively, a brain region could appear in this space even when it does not consistently have increased activation during any discrete emotion category per se, but because it has consistent increases during instances of the entire category *emotion* (e.g., the brain region shows consistent increases in activation in some but not all studies of *anger* experience, *anger* perception, *fear* experience, *fear* perception, and so forth, so that the region is consistently activated across the category *emotion*, but is not specific to any discrete emotion category). Our derived neural reference space for discrete emotion (Fig. 4; see also Table S3 in supplementary materials, available at: http://www.journals.cambridge.org/bbs2012008) closely resembles the one reported in Kober et al. (2008), even when limiting our analysis to studies of discrete emotion and including papers from 2006–2007. Next, we examined whether any emotion categories were more likely to be associated with increased activity in certain brain areas than in others.

4.1.2. Density analyses. Within the neural reference space, we first searched over the brain for voxels with more consistent activation (within 10 mm) for instances of one emotion category than for all others (e.g., for voxels that reached family-wise error-rate corrected significance in the comparison [*fear* perception vs. perception of other categories]). This analysis yielded a series of statistical maps reflecting whether each voxel was more frequently activated in studies of each emotion category versus the average of the others, accounting for the different numbers of studies in different categories and the base-rate of background activation across the brain for each emotion category. These analyses are standard for neuroimaging meta-analysis (see Wager et al. 2007) and are described in detail in the supplementary materials. The density analyses speak to whether increases in a brain region are consistently associated with the experience or perception of instances of an emotion category. This provides one kind of information about the consistency and specificity of brain activity for particular emotion categories by considering the activity in each

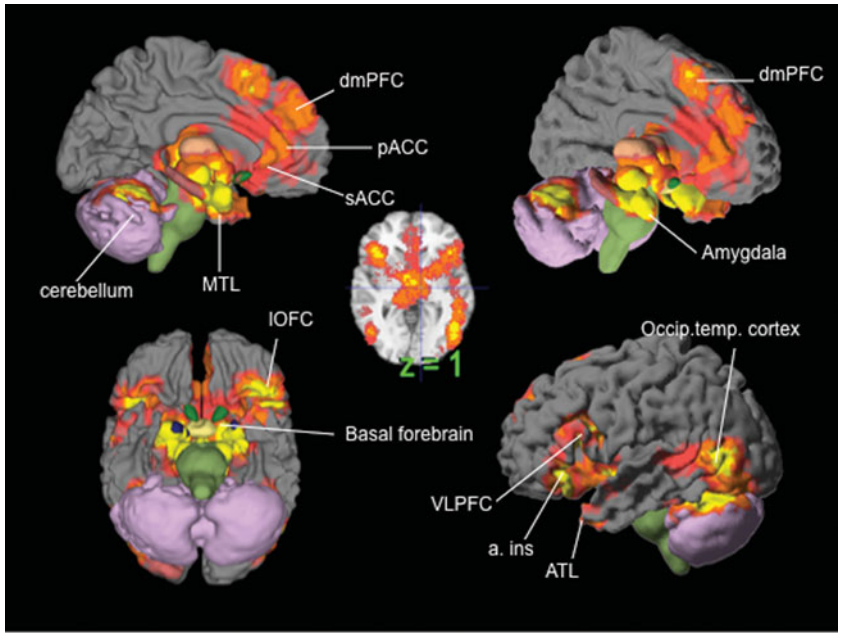

Figure 4. The Neural Reference Space for Discrete Emotion. The neural reference space (phrase coined by Edelman [1989]) is the set of brain regions consistently activated across all studies assessing the experience or perception of *anger, disgust, fear, happiness and sadness* (i.e. the superordinate category *emotion*). Brain regions in yellow exceeded the height threshold ($p < 05$) and regions in orange exceeded the most stringent extent-based threshold ($p < 001$). Regions in pink and magenta correspond to lesser extent-based thresholds and are not discussed in this article. Cortex is grey, the brainstem and nucleus accumbens are green, the amygdala is blue and the cerebellum is purple. A color version of this image can be viewed in the online version of this target article at http://www.journals.cambridge.org/bbs.

region, for each emotion type, *relative to* background activation levels across the brain.

4.1.3. χ^2 analyses. We next probed the voxels identified in the density analysis further by asking whether there was any *absolute* difference in the proportion of contrasts activating near those voxels (within 10 mm) for each emotion category versus the others. This was accomplished using χ^2 analyses on the contingency table consisting of counts of study contrasts showing activation in or around these voxels compared to study contrasts without such activations for the target emotion category versus other categories. This analysis yielded a series of statistical maps reflecting whether each voxel was more frequently activated in studies of each emotion category versus the average of the others, irrespective of activations elsewhere in the brain.

Both density and χ^2analyses speak to whether increased activations in a set of voxels that are consistently associated with the experience or perception of instances of an emotion category are also functionally selective[3] for that emotion category. A region that is functionally selective for instances of an emotion category would show voxels that are significant in both the density analysis and χ^2 analysis. Functional specificity exists if voxels activated selectively for instances of one emotion category also never show increased activity during instances of any other emotion categories. We did not find evidence for functional specificity with respect to any emotion category in our analyses (i.e., every region that was activated for one emotion category was activated for at least one other category). Therefore, our findings only speak to functional selectivity.

4.1.3. Logistic regressions. Finally, in a third set of analyses we used a series of stepwise logistic regressions to ask which emotion categories and experimental methods predicted increased activity in regions of interest. We present the odds ratios for these regressions (in Table S6 in the supplementary materials, available at http://www.journals.cambridge.org/bbs2012008) or the percent increase in odds that a variable predicted either increased activity in a brain area or no increase in a brain area (in Fig. 5).[4] The logistic regressions speak to both consistency and specificity of increased brain activation. Consistency is observed when any variable significantly predicted increased activity in a given brain area. Specificity is observed when one variable significantly predicted increased activity in a given brain area but all others significantly predicted no increase in activity. If a variable was not a significant predictor, then it is sometimes associated with increased activity, and is sometimes not.

5. Testing hypotheses of brain–emotion correspondence

5.1. The amygdala

According to a locationist hypothesis, the amygdala (Fig. 1, yellow) is either the brain locus of *fear* or is the most important hub in a *fear* circuit. This amygdala-*fear* hypothesis was most clearly popularized by behavioral neuroscience work showing that the amygdala (in particular, the central nucleus) supports the cardiovascular changes that occur when rats freeze or startle in response to tones previously paired with shock (called "fear learning":

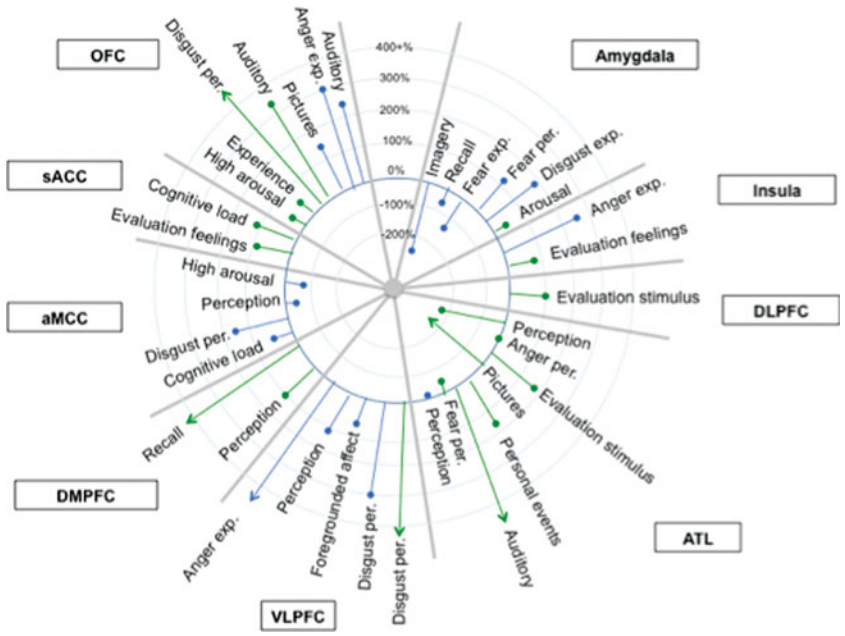

Figure 5. Logistic Regression Findings. Selected results from the logistic regressions are presented (for additional findings, see Table S6 in supplementary materials). Circles with positive values represent a 100% increase in the odds that a variable predicted an increase in activity in that brain area. Circles with negative values represent a 100% increase in the odds that a variable predicted there would not be an increase in activity in that brain area. **Legend:** Blue lines: left hemisphere; Green lines: right hemisphere. Arrowheads: % change in odds is greater than values represented in this figure. **Abbreviations:** OFC: orbitofrontal cortex; DLPFC: dorsolateral prefrontal cortex; ATL: anterior temporal lobe; VLPFC: ventrolateral prefrontal cortex; DMPFC: dorsomedial prefrontal cortex; aMCC: anterior mid-cingulate cortex; sAAC: subgenual ACC. A color version of this image can be viewed in the online version of this target article at http://www.journals.cambridge.org/bbs.

LeDoux et al. 1983; 1985; 1990; for reviews see Fanselow & Poulous 2005; Fendt & Fanselow 1999; LeDoux 2007; Öhman 2009; and "fear potentiated startle": Davis 1992; Hitchcock & Davis 1986; 1987; see Davis et al. 2008; Fendt & Fanselow 1999). Electrical stimulation of the amygdala elicits defensive behavior in rats (e.g., retreat; Maskati & Zbrozyna 1989) and enhances startle to acoustic stimuli (Rosen & Davis 1988). The amygdala-*fear* hypothesis was further strengthened by evidence that humans show increased amygdala activity to neutral tones that have been previously paired with noxious noise blasts (i.e., "fear learning"; LaBar et al. 1998). Individuals with amygdala lesions (LaBar et al. 1995) or atrophy (Bechara et al. 1995) show impaired skin conductance responses during "fear learning" and have difficulty perceiving instances of *fear* in voices (Brierley et al. 2004; Scott et al. 1997, but see, Adolphs & Tranel 1999; Anderson & Phelps 1998), bodies (Sprengelmeyer et al. 1999; but see, Atkinson et al. 2007), and startled faces with wide eyes (e.g., Adolphs et al. 1994; 1995; 1999; although see, Adolphs et al. 2005; Tsuchiya et al. 2009). An individual with bilateral amygdala lesions failed to report fearful experiences when placed in close contact with snakes, spiders, or when startled (Feinstein et al. 2011; although see, Anderson & Phelps 2002). Finally, the amygdala is implicated in psychopathology involving the experience of anxiety in humans (for a review, see Damsa et al. 2009; for a meta-analytic review, see Etkin & Wager 2007).

According to a psychological constructionist view, the amygdala is part of the distributed network that helps to realize core affect (Fig. 2, panel D, bright pink) because it is involved in signaling whether exteroceptive sensory information is motivationally salient (for similar views see Adolphs 2008; 2009; Duncan & Barrett 2007; Pessoa 2010b; Pessoa & Adolphs 2010; Sander et al. 2003; Whalen 2007; Whalen 1998). The amygdala is most likely to be active when the rest of the brain cannot easily predict what sensations mean, what to do about them, or what value they hold in that context. Salient objects or events influence an organism's body state in a way that can be experienced as core affective feelings (Barrett & Bliss-Moreau 2009). They can also cause the amygdala to signal to other parts of the brain to sustain processing so that uncertainty about the stimulus can be resolved (Whalen 2007). As a result, affect can be considered a source of attention in the brain (Barrett & Bar 2009; Duncan & Barrett 2007; Pessoa 2008; 2010b; Vuilleumier 2005; Vuilleumier & Driver 2007).

From a psychological constructionist point of view, *fear*-inducing stimuli might fall into the class of uncertain and therefore salient stimuli, but the amygdala is not specific to the category *fear*. Consistent with this view, the amygdala is routinely implicated in orienting responses to motivationally relevant stimuli (Holland & Gallagher 1999). Novel stimuli (e.g., Blackford et al. 2010; Breiter et al. 1996; Moriguchi et al. 2010; Schwartz et al. 2003; Weierich et al. 2010; Wilson & Rolls 1993; Wright et al. 2003; 2006; 2008), uncertain stimuli (e.g., Herry et al. 2007), and unusual stimuli (e.g., Blackford et al. 2010) robustly activate the amygdala and produce cardiovascular responses associated with affective changes (Mendes et al. 2007). Amygdala lesions disrupt normal responses to novelty and uncertainty in mammals (e.g. Bliss-Moreau et al. 2010; Burns et al. 1996; Mason et al. 2006; Missilin & Ropartz 1981; Nachman & Ashe 1974; for reviews, see Knight & Grabowecky 1999; Petrides 2007). Individuals with amygdala lesions do not automatically allocate attention to aversive stimuli (Anderson & Phelps 2001) and socially relevant stimuli (Kennedy & Adolphs 2010), as do individuals with intact amygdalae. Amygdala responses habituate rapidly (Breiter et al. 1996; Büchel et al. 1999; Fischer et al. 2003; Whalen et al. 2004; Wright et al. 2001), suggesting that the amygdala is involved in attention to salient stimuli, but calling into question the idea that the amygdala is necessary to *fear* per se (for a similar point, see Adolphs 2008; 2010; Pessoa & Adolphs 2010; Todd & Anderson 2009; Whalen 2007).[5]

The amygdala's role in detecting motivationally salient stimuli would also explain why increased amygdala activity is observed in instances that do not involve the experience of *fear*, such as when stimuli are experienced as subjectively arousing (e.g., Bradley et al. 2001; Weierich et al. 2010), intense (e.g., Bach et al. 2008), emotionally "impactful" (e.g., Ewbank et al. 2009), or valuable (Jenison et al. 2011). Moreover, not all instances of *fear* are accompanied by increased amygdala activity (for a review, see Suvak & Barrett 2011). For example, some behaviors that rats perform in dangerous contexts are not amygdala-dependent (e.g., avoiding the location of a threat: Vazdarjanova & McGaugh 1998; "defensive treading," where bedding is kicked in the direction of the threat: Kopchia et al. 1992). In humans, threatening contexts devoid of salient visual stimuli (e.g., preparing to give a speech in front of an audience), actually produce deactivatations in the amygdala (Wager et al. 2009a; 2009b). Moreover, electrical stimulation to the amygdala produces a range of experiences in humans, calling into question the idea that the amygdala is specifically linked to instances of *fear* (Bancaud et al. 1994; Gloor 1990; Halgren et al. 1978).

Our meta-analytic findings were inconsistent with a locationist hypothesis of amygdala function but were more consistent with the psychological constructionist hypothesis. Our density analyses revealed that, as compared to other brain regions, voxels within both amygdalae had more consistent increases in activation during instances of *fear* perception than during the perception of any other emotion category (Table 1). These voxels were not functionally specific for instances of perceiving *fear*, however. An insignificant χ^2 analysis revealed that the voxels with consistent increases in activation during instances of *fear* perception were equally likely to have increased activity during instances of other emotion categories (see Fig. 6 for the proportion of study contrasts in the database for each emotion category that are associated with increased activity in right [R] amygdala; see Fig. S2 in the supplementary material, available at http://www.journals.cambridge.org/bbs2012008, for left [L] amygdala). Furthermore, instances of *fear* experience did not show a consistent increase in activation in either amygdala when compared to what would be expected by chance in other regions of the brain. Yet, as compared to other brain regions, voxels within bilateral amygdala had more consistent increases in activation during instances of *disgust* experience than during the experience of other emotion categories (Table 1). A χ^2 analysis revealed that these voxels were functionally selective for of the experience of *disgust*, as there was more likely to be increased activity in those

Table 1. *Brain Regions with a Consistent Increase in Activity Associated with the Experience or Perception of Discrete Emotion Categories in Density Analyses*

Region	BA	Threshold	Contrast	Coordinates (MNI) x	y	z	Volume (voxels)
Amygdala-Fear Hypothesis							
L. Amygdala		*Height*	Disgust experience	−32	−2	−20	2
				−20	−4	−22	124
			Fear perception	−30	−2	−24	1
				−24	−2	−12	360
			Sad perception	−30	−4	−20	1
R. Amygdala		*Height*	Disgust experience	26	0	−22	121
			Fear perception	24	−4	−12	250
Insula-Disgust Hypothesis							
L. a. insula		*Height*	Anger experience	−42	22	−2	2
		Extent	Disgust perception	−26	22	−12	252
R. a. insula/R. lOFC		*Height*	Disgust perception	38	20	4	37
OFC-Anger Hypothesis							
L. lOFC	11	*Height*	Disgust experience	−30	36	−18	167
ACC-Sadness Hypothesis							
aMCC	24	*Extent*	Fear perception	−2	16	22	196
Conceptualization							
L. dorsal entorhinal	34	*Height*	Disgust experience	−16	2	−16	1
				−18	0	−14	1
		Height	Sad experience	−24	2	−12	19
L. hippocampus		*Height*	Sad perception	−28	−10	−20	1
R. dorsal entorhinal	34	*Height*	Anger perception	18	−12	−16	27
		Height	Fear perception	14	−6	−12	1
DMPFC	9	*Extent*	Happy experience	−2	44	20	324
		Height	Sad experience	2	50	38	1
Executive control							
R. VLPFC	44	*Height*	Disgust perception	46	18	10	71
L. VLPFC	9	*Height*	Anger perception	−52	12	24	27
R. DLPFC	9	*Height*	Anger perception	54	22	28	130
Exteroceptive Sensory Processing							
R. parastriate	18	*Height*	Anger perception	52	−76	−2	2
				48	−76	0	1
				42	−86	2	3
		Height	Fear experience	8	−96	4	10
L. peristriate	19	*Extent*	Anger perception	−48	−80	−8	197
L. occipitotemporal	37	*Height*	Disgust experience	−44	−58	−12	7
		Extent	Anger perception	−44	−54	−20	232
				−50	−62	6	254
R. occipitotemporal	37	*Height*	Anger perception	44	−56	−24	1
				40	−56	−20	1
				40	−54	−14	7
L. middle temporal	21	*Height*	Fear experience	−52	−70	8	72
		Extent	Sad perception	−66	−48	8	323
R. middle temporal	21		Sad experience	52	−10	−16	2
Uncus		*Height*	Fear perception	−30	4	−22	5
Other							
R. SMA	6	*Height*	Anger perception	44	−2	56	1
R. putamen		*Height*	Sad experience	26	4	−4	1
				28	8	−2	3
				22	4	−2	1
PAG		*Height*	Sad experience	0	−38	−10	1

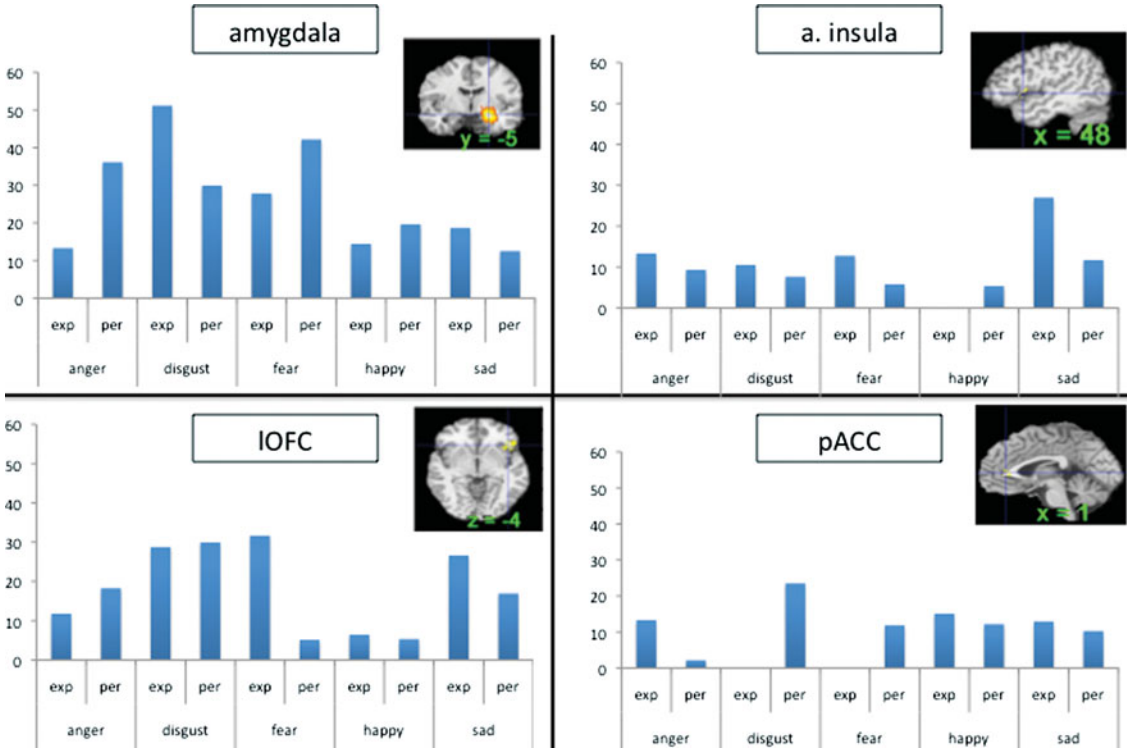

Figure 6. Proportion of Study Contrasts with Increased Activation in Four Key Brain Areas. The y-axes plot the proportion of study contrasts in our database that had increased activation within 10 mm of that brain area. The *x*-axes denote the contrast type separated by experience (exp) and perception (per). All brain regions depicted are in the right hemisphere. See Figures S2 and S3 in supplementary materials, available at http://www.journals.cambridge.org/bbs2012008, for additional regions. A color version of this image can be viewed in the online version of this target article at http://www.journals.cambridge.org/bbs.

voxels during instances of *disgust* experience than during the experience of *anger*, *fear*, *happiness* or *sadness* (Table 2). Those voxels were not functionally specific to instances of *disgust* experience, however (Fig. 6; Fig. S2). Finally, as compared to other brain regions, a voxel in L. amygdala had more consistent increases in activation during instances of *sadness* perception than during the perception of other emotion categories (Table 1). An insignificant χ^2 analysis revealed that this voxel was not functionally selective for instances of *sadness*, however.

Our logistic regressions confirmed and expanded upon our density and χ^2 findings. There was more likely to be increased activity in the L. amygdala when participants were perceiving instances of *fear* or experiencing instances of *disgust* than when perceiving or experiencing any other emotion categories (Fig. 5; Table S6). These findings are consistent with the psychological constructionist hypothesis that the amygdala responds to salient perceptual stimuli because contrasts in our database that assessed the perception of *fear* and experience of *disgust* tended to use visual stimuli that are novel or unfamiliar to participants.[6] Findings for the R. amygdala also supported a psychological constructionist view. Increases in activity in the R. amygdala were likely when participants were experiencing or perceiving instances of any highly arousing emotion category (i.e., *anger*, *disgust*, *fear*) (Fig. 5; Table S6). There was likely to be no increase in activity in the L. amygdala when participants were focusing on their internal state (i.e., when emotion experience was induced via recall of a personal event and mental imagery; Fig. 5; Table S6). This finding replicates prior meta-analytic evidence (Costafreda et al. 2008) and is consistent with our hypothesis that the amygdala responds preferentially to salient exteroceptive (vs. interoceptive) sensations.

5.2. The anterior insula

Locationist accounts hypothesize that the anterior insula (Fig. 1, green) is the brain basis of *disgust* (e.g., Jabbi et al. 2008; Wicker et al. 2003; for reviews, see Calder et al. 2001; Calder 2003) based on the belief that *disgust* evolved from a primitive food rejection reflex (Rozin et al. 2000) or bodily aversion to disease-threat (e.g., Curtis et al. 2004). Individuals with damage to the anterior insula and basal ganglia have difficulty perceiving instances of *disgust* in facial and vocal caricatures (Adolphs et al. 2003; Calder et al. 2000). They also report experiencing less *disgust* in response to scenarios about body products, envelope violation, and animals that typically evoke disgust in people with intact insulas (Calder et al. 2000). Individuals with neurodegenerative diseases affecting the insula and basal ganglia (such as Huntington's and Parkinson's disease) also show diminished experiences of *disgust* to foul smelling odors (Mitchell et al. 2005) and have difficulty perceiving instances of *disgust* in the faces of others (e.g., Kipps et al. 2007; Sprenglemeyer et al. 1996; 1998; Suzuki et al. 2006; see Calder et al. 2001; Sprengelmeyer 2007, for reviews), although the specificity of these findings remains in question (e.g., Calder et al. 2010; Milders et al. 2003). Patients who received electrical stimulation to the anterior insula reported visceral sensations consistent with (but not specific to) the experience of *disgust* (e.g.,

Table 2. *Brain Regions with a Consistent Increase in Activity Associated with the Experience or Perception of Discrete Emotion Categories in χ^2 Analyses*

Region	BA	Contrast	Coordinates (MNI) x	y	z	Volume (voxels)
Amygdala-Fear Hypothesis						
L. Amygdala		Disgust experience	−20	−6	−24	50
			−32	−2	−20	2
R. Amygdala		Disgust experience	26	2	−20	59
Insula-Disgust Hypothesis						
L. a. insula		Anger experience	−44	20	−2	1
R. a. insula		Disgust perception	42	14	4	4
			34	20	6	3
			36	18	2	1
OFC-Anger Hypothesis						
L. lOFC	11	Disgust experience	−30	36	−18	167
R. lOFC	47	Disgust perception	38	22	0	8
Other regions in the neural reference space						
Conceptualization						
L. entorhinal cortex	34	Disgust experience	−26	−6	−20	1
		Sad experience	−24	2	−12	10
R. entorhinal cortex	34	Anger perception	16	−10	−16	23
DMPFC	9	Sad experience	2	50	38	1
Executive attention						
L. VLPFC	9	Anger perception	−52	14	24	27
R. VLPFC	44	Disgust perception	46	20	10	66
R. DLPFC	9	Anger perception	54	22	28	130
Exteroceptive Sensory Processing						
R. parastriate	18	Anger perception	52	−76	−2	2
			48	−76	0	1
			42	−86	2	3
		Fear experience	8	−96	4	10
L. occipitotemporal	37	Disgust experience	−46	−58	−14	1
			−42	−58	−10	1
R. occipitotemporal	37	Fear experience	48	−72	2	127
		Anger perception	44	−56	−24	1
			38	−52	−14	6
L. middle temporal	21	Fear experience	−52	−70	8	72
R. middle temporal	21	Sad experience	52	−10	−16	2
Other						
R. SMA	6	Anger perception	44	−2	56	1
R. putamen		Sad experience	26	4	−4	1
			28	8	−2	3
			22	4	−2	1
PAG		Sad experience	0	−38	−10	1

sensations in the stomach or throat, smelling or tasting something bad, nausea; Penfield & Faulk 1955).

In a psychological constructionist hypothesis, the anterior insula plays a key role in representing core affective feelings in awareness (Fig. 2, panel D, dark pink). The anterior insula is thought to be involved in the awareness of bodily sensations (Craig 2002) and affective feelings (Craig 2009). Sometimes sensations from the body are experienced as physical symptoms, but more often they are experienced as states that have some hedonic tone and level of arousal. Sometimes those affective feelings are experienced as emotion. To the extent that brain states corresponding to instances of *disgust* represent a stimulus's consequence for the body, then the anterior insula will show increased activation. Indeed, a key ingredient in the mental states labeled "disgust" is likely a representation of how an object will affect the viscera. In support of a psychological constructionist view, anterior insula activation is observed in a number of tasks that involve awareness of body states, but not *disgust* per se. The anterior insula shows increased activation during awareness of body movement (e.g., Tsakiris

et al. 2007), gastric distention (e.g., Wang et al. 2008), and orgasm (e.g., Ortigue et al. 2007). Electrical stimulation of the insula produces sensations consistent with the category *disgust*, but it also produces a range of other visceral sensations including feelings of movement, twitching, warmth and tingling in the lips, tongue, teeth, arms, hands, and fingers (Penfield & Falk 1955). Dorsal anterior insula is also a hub in a large-scale network involved in what has been called a ventral attention system (Corbetta & Shulman 2002, Corbetta et al. 2008) that guides attention allocation and orienting (e.g., Eckert et al. 2009). These findings again point to the idea that body-based sensory signals constitute a source of attention in the brain.

Our meta-analytic findings were inconsistent with the locationist account that the anterior insula is the brain seat of *disgust* but were more consistent with the psychological constructionist account that insula activity is correlated with interoception and the awareness of affective feelings. Our density analyses revealed that as compared to other brain regions, voxels within the right [R.] anterior insula had more consistent increases in activation during instances of *disgust* perception than during the perception of any other emotion category (Table 1). Our χ^2 analysis revealed that only four of the voxels identified in the density analysis showed functional selectivity for instances of *disgust* perception (Table 2), however, and increased activity in R. insula was not specific to instances of *disgust* perception (Fig. 6). Our logistic regression findings for the R. anterior insula were consistent with the psychological constructionist hypothesis that the insula supports representation of core affective feelings. Increased activity in R. anterior insula was likely when participants were explicitly evaluating their feelings and representing them in awareness (Fig. 5, Table S6). Instances of *disgust* perception might consistently involve increased activation in the insula because people are more likely to simulate visceral states (such as those associated with the gut and food rejection) when perceiving facial behaviors characterized by a wrinkled nose and curled lip (i.e., oral revulsion; Angyal 1941; see also, Rozin et al. 2008; von dem Hagen et al. 2009).

As compared to other brain regions, a greater spatial extent of voxels within the left [L.] anterior insula had consistent increases in activation during instances of *disgust* experience than during the experience of any other emotion category (Table 1). As compared to other brain regions, two voxels in L. anterior insula also had more consistent increases in activation during instances of *anger* experience than during the experience of any other emotion (Table 1; only one voxel showed functional selectivity, see Table 2). Our logistic regressions replicated this general finding. Increased activity in L. anterior insula was more likely when participants were experiencing an instance of *anger* than when they were experiencing any other emotion category (Fig. 5; Table S6). These findings, along with subsequent findings (see sect. 5.3 for the orbitofrontal cortex, sect. 5.6 for the anterior temporal lobe and ventrolateral prefrontal cortex, and 5.7 for the dorsolateral prefrontal cortex) suggest that instances of *anger* are associated with increased activity in a broad set of areas in the left frontal and temporal lobes.

5.3. The orbitofrontal cortex

Locationist accounts link the orbitofrontal cortex (OFC) to *anger* (Fig. 1, rust), although the OFC is a large structure and has admittedly been linked to many other psychological phenomena. Primary support for the OFC-*anger* hypothesis derives from prior meta-analytic reviews of the neuroimaging literature (Murphy et al. 2003; Vytal & Hamann 2010). Studies using electroencephalography (EEG) also associate instances of *anger* with the prefrontal cortex (PFC).[7] Using EEG, activity in the left PFC is associated with instances of *anger* experience in response to an insult (Harmon-Jones & Sigelman 2001) and with the personality disposition to experience angry feelings (Harmon-Jones & Allen 1998). Other evidence for an OFC-*anger* hypothesis is more circumstantial. For instance, there is a body of evidence linking the OFC to aggression. It is far from clear that aggression is an unambiguous index of the entire category of *anger*, however. Nonhuman animals aggress in a number of different contexts (e.g., maternal aggression, sexual aggression, predatory aggression, defensive aggression; Moyer 1968); only some of which are associated with the concept called "anger" in English. Humans do a number of things in *anger*, only some of which constitute aggression. With that caveat, there is certainly evidence linking increased activity in the OFC to aggression. EEG activity in the left PFC is associated with an increased tendency to retaliate towards another person following an insult (by allocating him or her a dose of unpleasant hot sauce in a putative taste test; Harmon-Jones & Sigelman 2001). Aggressive behavior in rats is associated with increased activity in the ventral forebrain (including the OFC) (Ferris et al. 2008). Some lesion evidence is consistent with the idea that the OFC produces aggression in monkeys, because OFC lesions reduce aggression (towards humans: Butter & Snyder 1972; Kamback 1973; towards other monkeys: Raleigh et al. 1979). The majority of lesion studies find that monkeys (e.g., Deets et al. 1970; Machado & Bachevalier 2006; Raleigh et al. 1979) and rats (de Bruin et al. 1983) are more aggressive towards conspecifics following OFC lesions, however. Similarly, electrical stimulation of the lateral OFC (lOFC; in cats: Siegel et al. 1975) and the medial OFC (mOFC; in cats: Siegel et al. 1974; and in rats: de Bruin 1990) inhibits, rather than causes, aggressive behavior. Humans with lesions in the ventromedial PFC (which contains the OFC) become frustrated more easily and engage in more verbal (but not physical) aggression than do neurologically intact subjects (Grafman et al. 1996). Psychopathy and antisocial disorder are marked by increased aggression and correspond to structural (e.g., Raine et al. 2000) and functional (e.g., Glenn et al. 2009; Harenski et al. 2009) changes to the mOFC (Yang & Raine 2009). Fewer studies have linked the lOFC to aggressive behavior in humans, but one study found that individuals with borderline personality disorder who have lowered baseline lOFC (BA 47) activity are more likely to aggress against others (Goyer et al. 1994).

A psychological constructionist view hypothesizes that portions of the OFC play a role in core affect as a site that integrates exteroceptive and interoceptive sensory information to guide behavior. Together, sensory information from the world and sensory information from the body guide an organism's response to the environment and allow it to engage in behavior that is well tuned to the context (defined both by the external surroundings and the organism's goals). With the lOFC's connections to sensory modalities (e.g., Barbas 1988; Rolls 1999, see

Kringelbach & Rolls 2004) and the mOFC's connections to areas involved in visceral control (e.g., Carmichael & Price 1995; Eblen & Graybiel 1995; Ongür & Price 1998; 2000; Rempel-Clower & Barbas 1998; see Kringelbach & Rolls [2004] for a review), the OFC is anatomically well suited to perform this role. We are not claiming that this is the OFC's specific function, but only that it is a brain region that is important to realizing this function. Consistent with the idea that the OFC unites internal and external sensory information, the lOFC and the mOFC have been linked to associative learning (Rolls et al. 1994; 1996) decision making (e.g., Bechara et al. 1996; 2000; Koenigs et al. 2007) and reversal learning, in which the reward values associated with choice options are reversed and animals must learn the current reward value (Chudasama & Robbins 2003; Hornak et al. 2004; Rudebeck & Murray 2008). The inability to properly integrate exteroceptive and interoceptive information will result in behavior that is inappropriate to that context, explaining the altered non-aggressive social behavior (e.g., Beer et al. 2003; Eslinger & Damasio 1985; Saver & Damasio 1991; see Damasio et al. 1990) and aggression (Grafman et al. 1996) observed in individuals with OFC damage.

Our meta-analytic findings were inconsistent with the locationist hypothesis that the OFC is the brain seat of *anger*. As compared to voxels within other brain regions, voxels within the OFC did not have more consistent increases during instances of *anger* experience or perception than during any other emotion category. Rather, as compared to voxels within other brain regions, voxels within the left lOFC had more consistent increases in activation during instances of *disgust* experience than during the experience of other emotion categories (Table 1). Voxels within the right lOFC, as compared to voxels within other brain regions, had more consistent increases in activation during instances of *disgust* perception than during the perception of other emotion categories (Table 1). χ^2 analyses indicated that there was some functional selectivity for instances of *disgust* experience and perception in the voxels in the right and left lOFC that were respectively identified in the density analysis. Activity in the right and left lOFC was not specific to instances of *disgust* experience or perception, however (Fig. 6; Fig. S2). Our logistic regressions confirmed that when participants were perceiving an instance of *disgust*, there was more likely to be increased activity in the right lOFC than when participants were perceiving instances of any other emotion category (Fig. 5; Table S6).

Our logistic regressions revealed that increased activity in the left lOFC was more likely when participants were experiencing instances of *anger* than when experiencing instances of any other emotion category (Fig. 5; Table S6). Although in and of itself, this finding provides partial support for the OFC-*anger* hypothesis, our other meta-analytic findings indicate that increased activity in the left hemisphere during instances of *anger* is not restricted to the OFC, or even the prefrontal cortex (see sect. 5.2, "The anterior insula," sect. 5.6, "Anterior temporal lobe and ventrolateral prefrontal cortex," and sect. 5.7, "Dorsolateral prefrontal cortex"). Additionally, our logistic regressions revealed that increased activity in the left and right lOFC was likely when participants were experiencing a range of exteroceptive (auditory stimuli, visual pictures) and interoceptive (experience or perception of high-arousal core affect) sensations (Fig. 5; Table S6). This finding is consistent with the psychological constructionist hypothesis that OFC plays a more general role in integrating heteromodal sensations.

5.4. The anterior cingulate cortex

Locationist accounts hypothesize that pregenual anterior cingulate cortex (pACC; BAs 24, 32) and subgenual anterior cingulate cortex (sACC; BA 25) are the brain basis of *sadness* (Fig. 1, blue). The pACC and sACC have known affective function and are thought to instantiate the visceromotor responses observed during classical conditioning, pain, and affective behaviors (Devinksy et al. 1995; Vogt 2005). The ACC-*sadness* hypothesis, like the OFC-*anger* hypothesis, derives support from prior meta-analyses of the neuroimaging literature (e.g., Murphy et al. 2003; Phan et al. 2002). In the behavioral neuroscience literature, pACC has been linked to *sadness* because of its role in producing the vocalizations that infant animals make when separated from their mother (e.g., MacLean & Newman 1988; see Panksepp 1998; 2007); the link between infant vocalizations and unpleasant affect are in question, however (Blumberg & Sokoloff 2001). One study in humans found that pACC lesions (including lesions to dorsomedial prefrontal cortex) produce hypersensitivity and an increased tendency to cry at sad events (Hornak et al. 2003). If the pACC were involved in instantiating instances of *sadness*, then lesions to this structure should abolish the tendency to cry at sad events. These findings are therefore more consistent with the idea that pACC regulates instances of *sadness*. Finally, pACC is implicated in pain, perhaps because it supports the feeling of "suffering" (cf. Vogt 2005). The sACC, on the other hand, has been linked to *sadness* because of its role in depression. Clinical depression is marked by structural and functional changes in sACC (see Gotlib & Hamilton [2008] for a review), although clinical depression involves many symptoms above and beyond the experience of *sadness* (Coyne 1994). Electrical stimulation of the sACC relieves intractable depression by reducing feelings of apathy and anhedonia, normalizing sleep disturbances, and decreasing gross motor impairments (e.g., Mayberg et al. 2005).

Our psychological constructionist hypothesis draws on the neuroscience literature showing that pACC, sACC, and the more dorsal anterior midcingulate cortex (aMCC) (Vogt 1993; Vogt et al. 2003) take part in distinct psychological operations related to realizing core affect. In our view, the pACC and sACC (along with the adjacent posterior mOFC) are cortical sites for visceral regulation that help to realize a core affective state during motivated action (Devinksy et al. 1995) (Fig. 2, panel B, light pinks). We would therefore predict increased activation in pACC and sACC across a variety of emotional instances. The hypothesized role of sACC in regulating somatovisceral states could explain why sACC is involved in the affective changes that accompany both depression (e.g., Drevets et al. 1992; see Gotlib & Hamilton 2008) and mania (e.g., Fountoulakis et al. 2008), and why electrical stimulation of this region helps to relieve chronic depression (Mayberg, et al. 2005). The aMCC (Fig. 2, panel B, dusty pink) is hypothesized to play a role in executive attention and motor engagement during response

selection (Mansouri et al. 2009; Rushworth et al. 2007). In this view, aMCC delivers sources of exteroceptive sensory information (from thalamic projections; Barbas et al. 1991) and internal sensory information (from the insula; Mesulam & Mufson 1982) to direct attention and motor responses (via projections to lateral PFC and the supplementary motor area; e.g., Barbas & Pandya 1989; for reviews, see Devinsky et al. 1995; Paus 2001). These anatomical connections can explain why the aMCC is part of an intrinsic brain network that shows increased activity when stimuli in the environment are personally salient (Seeley et al. 2007). They also explain why the aMCC is responsible for resolving action selection during situations involving conflicting sensory information (e.g., Grinband et al. 2011; Milham et al. 2001; Nelson et al. 2003; see Banich 2009; Shackman et al. 2011; van Snellenberg & Wager 2009). By extension, as a visceromotor (i.e., autonomic) control area sACC/pACC might be involved in resolving which sensory inputs influence the body when there are multiple sources of sensory input that can influence an organism's body state.

Our meta-analytic evidence is inconsistent with the locationist account that the ACC is the brain basis of *sadness*, but more consistent with a psychological constructionist hypothesis of ACC function. As compared to voxels within other brain regions, voxels within the sACC, pACC and aMCC did not have more consistent increases when participants were experiencing or perceiving instances of *sadness* than during any other emotion category (Fig. 6). As compared to voxels within other brain regions, a greater spatial extent of voxels within the aMCC had consistent increases in activation during instances of *fear* perception than the perception of any other emotion category (Table 1). The amygdala, which responds to motivationally salient exteroceptive sensory stimuli (see sect. 5.1 "The amygdala"), projects to this area of aMCC (Vogt & Pandya 1987), so it is possible that increased activity here reflects response preparation to salient stimuli in the environment.

Our logistic regressions revealed that increases in sACC were likely when participants were engaged in cognitive load (Fig. 5; Table S6). Cognitive load typically occurred in studies where participants were asked to attend to core affective feelings (e.g., focus on their feelings, rate their feelings) or affective stimuli (e.g., focus on an affective stimulus, rate a stimulus' emotional value) and so it is possible that this finding is indicative of the sACC's role in instantiating core affective feelings. Increased activity in the sACC was marginally ($p < 0.09$) likely when participants were evaluating their feelings, again consistent with this area's role as a visceromotor regulation site. Finally, consistent with a response selection hypothesis of aMCC function, increased activity in the aMCC was likely when participants were engaged in cognitive load (Fig. 5; Table S6).

5.5. Dorsomedial prefrontal cortex, medial temporal lobe, and retrosplenial cortex/posterior cingulate cortex

Our psychological constructionist approach hypothesizes that a range of other brain regions are important to realizing instances of emotion experience and perception, including dorsomedial prefrontal cortex (DMPFC), ventromedial prefrontal cortex (VMPFC), medial temporal lobe (MTL), and retrosplenial cortex/posterior cingulate cortex (PCC) (Fig. 2, panel B, purples), which are associated with the psychological operation of conceptualization. As part of the process of making meaning out of sensory cues, we hypothesize that these brain areas use stored representations of prior experiences to make meaning of core affective inputs that come from the self or observing others. Locationist views do not hypothesize specific roles for these brain regions in emotion because they are usually considered to have a "cognitive" function, insofar that they support memory (Vincent et al. 2006), object perception (Bar 2009), and theory of mind (Mitchell 2009). In our view, these brain regions should not necessarily be more involved in instances of one category of emotion than another, although we would expect them to be part of the more general neural reference space for discrete emotion.

As we predicted, our meta-analytic results revealed that regions of the conceptualization network such as DMPFC, MTL, and retrosplenial cortex (Buckner et al. 2008) were part of the neural reference space for discrete emotion (Fig. 4).[8] Our findings indicate that the conceptualization network is integral in the experience and perception of discrete emotions, and are consistent with the hypothesis (in Barrett 2006b; 2009a; 2009b) that prior episodic experience helps shape experienced or perceived affect into meaningful instances of *emotion*.

Despite general involvement in emotion (Fig. 1; Fig. S3), there was some functional selectivity for instances of certain emotion categories in hubs within the conceptualization network. For instance, across our density analyses and logistic regressions, we found that instances of the experience of *sadness* (Tables 1 & 2) and experience of *happiness* (Table 1) were each associated with relatively greater consistent increases in activation in areas of DMPFC than other emotion categories. Consistent with the role of conceptualization in simulating episodic experience (Schacter et al. 2007), our logistic regressions revealed that increased activity in DMPFC was likely when participants were engaging in emotion inductions involving recall and films (Fig. 5). Increased activity in some clusters of DMPFC was likely when participants were perceiving *emotion* in faces, bodies or voices. This finding is consistent with the psychological constructionist hypothesis that the conceptualization network is brought to bear when affective facial behaviors are perceived as emotional. Other clusters of DMPFC showed an opposite pattern: When participants were perceiving *emotion*, increased activity in DMPFC was not likely (Table S6). Just as perception of others and self-referential thinking involve overlapping yet distinct aspects of DMPFC (Ochsner et al. 2004a), some aspects of DMPFC might be functionally selective for conceptualization during emotion perception whereas others support conceptualization during emotion experience.

Several emotion categories were also associated with consistent increases in activation in the MTL (Tables 1 & 2; see Table S6). Our logistic regressions revealed that, as in the DMPFC, increased activity in the right hippocampus was likely to occur when participants perceived any instance of *emotion* in a face, body, or voice. Increased activity in the left hippocampus, on the other hand, was likely to occur when participants perceived instances of

fear (Table S6). This finding is more likely to be related to the encoding of salient stimuli in memory than simulating prior experiences, as the amygdala also had increased activity during instances of *fear* perception and is known to have functional connectivity with the hippocampus during encoding of salient stimuli (Kensinger & Corkin 2004).

5.6. Anterior temporal lobe and ventrolateral prefrontal cortex

According to a psychological constructionist account, networks supporting language (e.g., Vigneau et al. 2006) should consistently show increased activity during instances of *emotion* experience and perception as linguistically-grounded concepts are brought to bear to make meaning of core affective feelings. In locationist accounts, language is thought to be epiphenomenal to discrete *emotion* (Ekman & Cordaro 2011), although recent behavioral studies show that categorical perception of discrete emotion is supported by language (Fugate et al. 2010; Roberson & Davidoff 2000; Roberson et al. 2007).

Consistent with the psychological constructionist view, nodes within networks supporting language were part of the neural reference space for discrete emotion (Fig. 4) In particular, the anterior temporal lobe (ATL) and ventrolateral prefrontal cortex (VLPFC) (Fig. 2, Panels A, B, C, green) had consistent increases in activity across studies of discrete emotion. The ATL supports language as a heteromodal association area involved in the representation of concepts (Lambon Ralph et al. 2009; Pobric et al. 2007; Rogers et al. 2004) and the right ATL has been implicated in the representation of abstract social concepts (e.g., Zahn et al. 2009). Patients with semantic dementia have focal atrophy to the ATL, difficulty utilizing semantic knowledge, and exhibit deficits in emotion perception (Rosen et al. 2004) and empathy (Rankin et al. 2006). Areas of the VLPFC, on the other hand, are implicated in semantic processing tasks (e.g., Gitelman et al. 2005), categorization of objects (e.g., Freedman et al. 2001), representation of feature-based information for abstract categories (e.g., Freedman et al. 2002; see Miller et al. 2002), selection amongst competing response representations (e.g., Badre & Wagner 2007; Schnur et al. 2009), and inhibition of responses (Aaron et al. 2004). It is therefore not clear that the VLPFC's role is functionally specific to language, but it is certainly functionally selective for language in certain instances. The VLPFC also helps comprise the ventral frontoparietal network that is thought to be involved in directing attention to salient stimuli in the environment (Corbetta & Shulman 2002; Corbetta et al. 2008), suggesting a more general role for this region in executive attention.

As compared to other brain regions, voxels within the ATL did not have more consistent increases during instances of one emotion category than others (Fig. S3). Our logistic regressions suggested that increased activity in the left ATL was more likely when participants were experiencing an instance of *anger* than any other emotion category, however (Fig. 5; Table S6). Instances of *anger* experience thus involve areas throughout the left frontal and temporal lobes (see sect. 5.2, "The anterior insula," sect. 5.3, "The orbitofrontal cortex," and sect. 5.7, "Dorsolateral prefrontal cortex"). Increased activity in the right ATL, on the other hand, was likely when participants were evaluating a stimulus (i.e., determining the emotional meaning of a face, voice, or picture; Table S6). This finding is consistent with the hypothesis that language is brought to bear when constructing emotional percepts from exteroceptive sensations.

Our density analyses revealed that as compared to voxels within other brain regions, voxels within the right VLPFC had more consistent increases during instances of *disgust* perception than during the perception of any other emotion category; these findings were confirmed with a logistic regression (Table 1; Table S6). χ^2 analyses revealed that a subset of the voxels identified in the density analysis were functionally selective for instances of *disgust* perception (Table 2), although they were not specific to instances of *disgust* (Fig. S3). The most common finding across our logistic regressions linked increases in the left VLPFC to instances in which participants were explicitly paying attention to emotional information (Fig. 5; Table S6). As in other left frontal and temporal areas (see sects. 5.2, "The anterior insula," 5.3, "The orbitofrontal cortex," 5.6, "Anterior temporal lobe and ventrolateral prefrontal cortex"), increased activity in the left VLPFC was likely when participants were experiencing or perceiving instances of *anger*.

5.7. Dorsolateral prefrontal cortex

According to a psychological constructionist account, networks supporting executive attention (see Miller & Cohen 2001; Petrides 2005; for a meta-analysis, see Wager & Smith 2003) should consistently show increased activity during instances of *emotion* experience and perception because executive attention directs other psychological operations during the construction of emotion. Locationist accounts do not propose specific roles for these networks in emotion, although they might allow that networks supporting executive attention take part in regulation of emotion after it is generated (as in Ochsner et al. 2004b; Urry et al. 2006).[9]

Consistent with our psychological constructionist hypothesis, nodes within networks supporting executive attention were part of the neural reference space for discrete emotion. In particular, the VLPFC and dorsolateral prefrontal cortex (DLPFC) (Fig. 2, Panel A, orange and striped green/orange) had consistent increases in activity across studies of discrete emotion. The DLPFC is part of the dorsal frontoparietal network that is thought to be involved in top-down, goal-directed selection for responses (Corbetta & Shulman 2002; Corbetta et al. 2008). Consistent with this functional connectivity, bilateral DLPFC is known to be involved in working memory (e.g., Champod & Petrides 2007; Constantinidis et al. 2002) and in the goal-directed control of attention (e.g., Rainer et al. 1998; see Miller 2000).

We predicted that DLPFC would be part of the neural reference space for emotion (Fig. 4) because these voxels would be active during mental states in which participants attended to emotional feelings or perceptions (i.e., when participants had to hold affective information in mind in order to categorize it). Consistent with this prediction, increased activity in the right DLPFC was likely when participants were explicitly evaluating stimuli (Fig. 5; Table S6). Our density analyses also revealed that as

compared to voxels within other brain regions, voxels in the right DLPFC were more likely to have increased activity during instances of *anger* perception than any other emotion categories (Table 1). Our χ^2 analyses indicated that some of these voxels were functionally selective to perceiving instances of *anger* (Table 2), although they were not specific to perceiving instances of *anger* (Fig. S3).

5.8. The periaqueducal gray

The periaqueducal gray (PAG) is involved in regulating the autonomic substrates that allow for behavioral adaptations such as freezing, fleeing, vocalization, and reproductive behavior (e.g., Carrive et al. 1989; Behbehani 1995; Gregg & Siegel 2001; Kim et al. 1993; Lovick 1992; Mobbs et al. 2007; Van der Horst & Holstege 1998) and also sends projections back to cortical sites involved in the regulation of visceral activations in the body (An et al. 1998; Mantyh 1983). It is believed that certain adaptations are associated with certain emotion categories (e.g., animals freeze in *fear*, aggress in *anger*) but such links are far from empirically clear. Humans (like other mammals) do many things during instances of *anger*, for example. Sometimes humans yell, sometimes they hit, sometimes they remain very still, and sometimes they smile. Even rats do many things within a single emotion category: In the face of a threat, rats can freeze (e.g., LeDoux et al. 1990), flee (Vazdarjanova & McGaugh 1998), or engage in "defensive treading," where they kick bedding in the direction of a known threat (Reynolds & Berridge 2002; 2003; 2008). In all these instances, PAG activity and the associated autonomic states it produces, are yoked to the action, and not to the emotion category. As a result, a psychological constructionist approach views PAG activity as nonspecifically involved in instances of emotion. A locationist approach has linked the PAG to distinct circuits corresponding to several emotion categories: *rage*, *fear*, *joy*, *distress*, *love* and *lust* (Panksepp 1998). In a psychological construction approach, the assumption is that a given dedicated circuit for a specific behavioral adaptation (e.g., withdrawal) will be active across a range of emotion categories (e.g., a person can withdraw in instances of both *fear* and *anger*), and different dedicated circuits within the PAG (e.g., fight, flight) will be active within instances of a single emotion category depending upon which behavioral adaptation is more relevant for the immediate context.

Testing any hypothesis about the specificity of a subcortical region like the PAG is practically impossible, given the spatial and temporal limitations of brain imaging. Still, it is instructive to note that the PAG was consistently activated within the neural reference space for discrete emotion (even though subjects were lying still and not engaging in any overt physical action; see Fig. S4 in the supplementary materials, available at http://www.journals.cambridge.org/bbs2012008). Moreover, we did not find evidence of functional specificity for the PAG in our meta-analysis. It is possible that given the resolution problems, different circuits within the PAG were specifically active for discrete emotions. That said, it is also entirely plausible from the behavioral data that humans, like animals, perform a range of actions within a single category, and perform the same action at times across categories (even if it does not match our stereotypes of *emotion*–action links). In this meta-analysis, increased activity in the PAG did not correspond to any particular emotion category more than another (although instances of the experience of *sadness* were associated with consistent increases in activation in one voxel within ventral PAG; Tables 1 & 2). The logistic regressions demonstrated that increased activity in the PAG was likely when participants were experiencing or perceiving an instance of any high-arousal emotion category (Table S6). Consistent with this finding, activity in a separate cluster of PAG was likely when participants were experiencing instances of *fear* (Table S6). In a previous meta-analysis, we found that the PAG was most likely to have increased activity during unpleasant emotions (Wager et al. 2008). Since all high-arousal emotion categories in our database were unpleasant (e.g., *fear*, *anger*, *disgust*), our present findings are consistent with Wager et al. (2008). Future research should probe whether the PAG preferentially shows increased activity during unpleasant states, highly aroused states, or during states that are both unpleasant and highly aroused.

5.9. Visual cortex

From our psychological construction approach, we would not be surprised to observe that voxels within visual cortex (or any sensory modality) show increased activation during emotion. In its most basic form, our hypothesis is that emotion emerges as a situated conceptualization of internal sensations from the body and external sensations from the world to create a unified conscious experience of the self in context. In fact, regions of visual cortex were some of the most frequent to appear in our meta-analytic findings (replicating several recent meta-analyses; e.g., Fusar-Poli et al. 2009; Kober et al. 2008; Vytal & Hamann 2010). It is beyond the scope of this article to discuss these findings in detail, but we found that instances of *fear* experience, *anger* perception, and *disgust* experience were consistently associated with increased activity in regions of visual cortex ranging from V2 to visual association cortex (Tables 1 & 2). Our logistic regressions revealed that activation in visual cortex was not merely a by-product of the methods used. Although increased activity in visual cortex was likely when visual methods were used (e.g., pictures, faces, studies of perception; see Table S6), it was also likely in studies of unpleasant, high-arousal emotions (e.g., *fear*, *disgust*, unpleasant emotions more generally; Table S6). Together, these findings indicate that experiences or perceptions of unpleasant emotion categories are realized by brain states that include increased activity in visual cortex. See Gendron et al. (in preparation) for a discussion.

6. Conclusion

Over a century ago, William James wrote, "A science of the relations of mind and brain must show how the elementary ingredients of the former correspond to the elementary functions of the latter," (James 1890/1998, p. 28). James believed that *emotions*, *thoughts*, and *memories* are categories derived from commonsense with instances that do not require special brain centers. With respect to *emotion*, he wrote, "sensational, associational, and motor

elements are all that [the brain] need contain" to produce the variety of mental states that correspond to our commonsense categories for emotion (cf. James 1890/1998, p. 473). James' view foreshadowed modern psychological constructionist models of the mind and the findings of our meta-analytic review, which are largely in agreement with this approach. Our findings are consistent with the idea that emotion categories are not natural kinds that are respected by the brain. The fact that some of the regions we report also appear in meta-analyses of other task domains (e.g., action simulation and perception, Grezes & Decety 2001; autobiographical memory, Svoboda et al. 2006; decision making, Krain et al. 2006; executive control, Owen et al. 2005; Wager & Smith 2003; Wager et al. 2004; language, Vigneau et al. 2006; self-referential processing, Northoff 2006) means that these regions are not specific to *emotion* per se, and are also involved in constituting other cognitive and perceptual events (for a discussion of domain general networks, see Dosenbach et al. 2006; Nelson et al. 2010; Spreng et al. 2009; van Snellenberg & Wager 2009). Such findings show that even categories like *emotion*, *cognition*, and *perception* are not respected by the brain (Barrett 2009a; Duncan & Barrett 2007; Pessoa 2008).

In keeping with James' predictions, our meta-analytic review did not find strong evidence for a locationist hypothesis of brain–emotion correspondence (see Table 3 for a summary of findings). In all instances where a brain region showed consistent increases in activation during instances of a discrete emotion category (e.g., the amygdala in instances of *fear* perception), this increase was not specific to that category, failing to support a key locationist assumption. Some brain regions showed functional selectivity for instances of certain emotion categories; these findings perhaps point to differences in the contents of mental states (e.g., instances of *anger* experience often involve approach motivation, instances of *disgust* perception often involve simulation of bodily activation, and instances of *fear* perception often involve detection of unusual and hence salient stimuli).

Our meta-analytic findings were relatively more consistent with the psychological operations that we have considered ingredients of emotion here and in other papers (e.g., Barrett 2006b; 2009; Barrett et al. 2007a; Kober et al. 2008; Lindquist & Barrett 2008a; Wager et al. 2008). In Kober et al. (2008), we hinted at the existence of basic psychological operations in the psychological construction of emotion. In other theoretical discussions (Barrett 2009) we explicitly hypothesized the need for mid-level scientific categories that describe the most basic psychological ingredients of the mind by referencing both biology and folk psychology when explaining how mental states like emotion experiences and perceptions arise (for a similar view, see Cacioppo et al. 2008). This target article is the first to investigate the extent to which brain regions associated with basic psychological domains show consistent increases in activation in neuroimaging studies of discrete emotion categories, despite a range of methodological variables. Of course, more work needs to be done to hone and refine our conceptions of the operations that are most psychologically primitive and to map them to networks in the brain, but this is a start.

Most notably, we observed consistent increases in activation in the brain regions implicated in conceptualization

Table 3. *Summary of Brain Regions Showing Consistent Increases in Activation During Mental States and Methodological Manipulations*

	Variable	Area
Mode	*Experience of emotion*	**R. lOFC**
	Perception of emotion	**DMPFC/dACC** **R. hippocampus** **L. VLPFC** **R. peristriate** **R. occipitotemporal**
Affect	*High arousal emotions*	**R. amygdala** **R. lOFC** **PAG**
	Unpleasant emotions	**L. peristriate**
Emotion	*Anger experience*	**L a. ins.*** **L. a. ins.** **L. lOFC** **L. VLPFC** **L. ATL**
	Anger perception	**L. VLFPC*** R. entorhinal cortex R. DLPFC R. parastriate R. occipitotemporal R. supplementary motor area
	Disgust experience	**L. amygdala*** R. amygdala L. entorhinal cortex **R. lOFC** **L. occipitotemporal***
	Disgust perception	**R. lOFC*** R. a. ins **aMCC** **L. VLPFC** **R. VLPFC*** **R. peristriate** **R. occipitotemporal**
	Fear experience	**PAG** **R. peristriate** R. parastriate **R. occipitotemporal*** L. middle temporal
	Fear perception	**L. amygdala** **L. entorhinal cortex** **R. entorhinal cortex** **L. hippocampus** **R. middle temporal**
	Happiness experience	**L. peristriate**
	Sadness experience	L. entorhinal cortex DMPFC R. middle temporal R. putamen

(*continued*)

Table 3 (*Continued*)

	Variable	Area
Method Types	*Recall*	PAG **pACC** **DMPFC/aMCC**
	Auditory	**R. lOFC** **R. VLPFC** **R. ATL**
	Imagery	**R. occipitotemporal** **R. middle temporal**
	Visual	**R. peristriate** **L. occipitotemporal**
Stimuli	*Pictures*	**L. lOFC** **R. peristriate** **R. occipitotemporal**
	Faces	**L. VLPFC**
	Films	**DMPFC/aMCC** **L. peristriate** **R. occipitotemporal** **R. middle temporal**
Other Psychological Variables	*Evaluation of feelings*	**R. a. ins** **sACC**
	Evaluation of stimulus	**R. ATL** **R. DLPFC** **PAG** **L. peristriate** **L. occipitotemporal**
	Foregrounded affect	**L. VLPFC** **L. peristriate**
	Cognitive load	**sACC** **aMCC**

Mental states include states related to experiencing vs. perceiving discrete emotions, the experience and perception of affect, the experience or perception of individual discrete emotion categories, and mental states related to method types, stimulus types and other psychological variables. Brain regions consistently associated with mental states in the χ^2 analyses and logistic regressions are listed. Mental state-brain associations observed in the χ^2 analyses are printed in regular font. Logistic regression findings are in bold face font. Mental state-brain region associations observed in both types of analyses are marked with an asterisk (*).

(simulation of prior episodic experiences), language (representation and retrieval of semantic concepts), and executive attention (volitional attention and working memory), suggesting that these more "cognitive" functions play a routine role in constructing experiences and perceptions of emotion. For example, increased activation in the DMPFC was observed when participants perceived instances of *emotion* on others' faces. Increased activation in the ATL was observed when participants focused on emotional stimuli. Increased activity in the VLPFC occurred when participants focused on the affective content of feelings or perceived instances of *emotion* on another person's face. Increased activity in the DLPFC occurred when participants evaluated the emotional content of a stimulus. One interpretation of these findings is that they are merely the result of the types of psychological tasks participants are asked to perform in the scanner during neuroimaging studies of emotion (e.g., recall, labeling, response selection), and that because of the limits of neuroimaging, these influences cannot be separated from an emotion itself. Yet, all data in our meta-analysis were derived from emotion versus neutral contrasts, meaning that, regardless of the task at hand, activation in these brain areas was greater when participants were experiencing or perceiving an emotion category than when they were experiencing or perceiving in a neutral control state. Activity in these brain regions is therefore integral to producing instances of *emotion*.

Our findings suggested the need to refine and add additional psychological operations to our model. Just as executive attention has been parsed into a set of distinguishable networks (e.g., Corbetta & Shulman 2002; Corbetta et al. 2008; Dosenbach et al. 2007; Seeley et al. 2007), we might further refine core affect into a set of smaller networks that correspond to even more basic mechanisms. For example, we might find separable networks corresponding to approach versus avoidance-related states. Our findings hint that brain regions in the left PFC might be candidates for a network involved in approach motivation because regions in the left lateral PFC (including the anterior and mid-insula, VLPFC, DLPFC and OFC) were consistently observed during instances of the experience of *anger*. This hypothesis is consistent with a large body of EEG evidence associating the left PFC with the experience of instances of *anger* (Harmon-Jones & Allen 1997; Harmon-Jones & Sigelman 2001) and approach motivation more generally (Amodio, et al. 2008; Fox 1991; Sutton & Davidson 1997). Future meta-analytic investigations should investigate the degree to which the left PFC and subcortical regions supporting incentive salience (e.g., ventral tegmentum, amygdala, and aspects of the nucleus accumbens and ventral pallidum; see Berridge & Robinson 2003) comprise a network for approach-related affect within the operation of core affect. We might also add ingredients for processing exteroceptive sensory sensations to our theoretical framework since visual cortex was one of the most frequently activated brain regions in our meta-analysis of discrete emotions. Exteroceptive sensory sensations are also important components of other types of mental states (e.g., perception, memory, judgments).

6.1. Alternate interpretations

Of course, there are alternate explanations for why we did not find strong evidence in support of a locationist framework. First, it is possible that neuroimaging is not well suited to yield evidence for functional specialization for emotion in the brain because of its spatial limitations. It therefore remains possible that scientists will find functional specialization for emotion at a more refined level of spatial analysis (e.g., at the level of smaller circuits or even cortical columns of neurons). While this always remains a possibility, it is important to note that even the most highly specialized brain regions (e.g., primary visual cortex) contain neurons that participate in different neural assemblies associated with different functions

(e.g., Basole et al. 2003). This makes strong locationist interpretations of brain function unlikely when such interpretations attempt to find specificity for psychological categories (particularly at the level of the cortical column). Instead, the idea of neural re-use (e.g., Anderson 2010) is consistent with the psychological constructionist model of brain–emotion correspondence. Neuroimaging also has temporal limitations. It takes a few seconds for a BOLD response to materialize and we do not know whether emotions are episodes that extend over many seconds or are more instantaneous states that fire and resolve within that time frame. It is possible that scientists might find functional specialization for emotion at a more refined level of temporal analysis (e.g., using single cell recording), although such evidence has yet to be revealed. Moreover, we find it unlikely that neuroimaging and single cell recordings are measuring totally different phenomena. More likely, they are methods that complement one another (e.g., Horowitz 2005).

Second, it remains a possibility that we failed to locate a specific brain basis for discrete emotion categories because emotion categories are represented as anatomical *networks* of brain regions. Some researchers hypothesize that "resting state" analyses[10] of the brain's function, which reveal the intrinsic anatomical networks that chronically support the brain's fundamental processes, are influenced by anatomical connections (Deco et al. 2011). If emotion categories were supported by anatomically given, inherited networks, then there should be intrinsic networks that correspond to the brain regions active during the experience or perception of instances of *anger*, *sadness*, *fear*, and other emotion categories. To date, however, no such intrinsic networks have been identified in broad inductive studies of such brain organization (e.g., Smith et al. 2009). Instead, the intrinsic networks that have thus far been identified bear resemblance to the psychological domains that are hypothesized by a psychological constructionist view (see functional groups in Kober et al. 2008). For instance, the "default network" that is active when a person is not probed by an external stimulus in fMRI experiments (Buckner & Vincent 2007; Raichle et al. 2001) is not only important to constructing representations of the past and the future, but also for constructing representations of emotion experience and perception in the moment. Portions of the intrinsic networks for "personal salience" (e.g., Seeley et al. 2007) and "executive control" (e.g., Corbetta & Shulman 2002; Seeley et al. 2007) appear anatomically similar to brain regions that we observed within our meta-analyses as well.

Of course, there is evidence for more limited brain circuits that correspond to specific behavioral adaptations in mammals. There is well-documented evidence for the anatomical circuitry underlying specific actions such as vocalizations (Jürgens 2009), maternal behavior (e.g., pup retrieval, grooming, nest building, and nursing; Numan 2007), freezing (Fanselow & Poulos 2005), startle (Davis et al. 2008; Lang et al. 2000), attack (Blanchard & Blanchard 2003) and appetitive behavior (Berridge & Kringelbach 2008; Shultz 2006), to name just a few. In our view, these are just another set of basic operations and are not, in and of themselves, evidence that there is distinct anatomical circuitry for complex psychological categories such as *sadness*, *love*, *fear*, *anger*, or *greed* (each of which could contain instances of a range of behaviors) (Barrett et al. 2007a). Animals produce actions in a way to maximize their outcome in a specific context, so many different behaviors can be associated with a given discrete emotion category; there is variety in the behaviors and the autonomics that populate any given emotion category. Sometimes, to make their findings more accessible, researchers will equate a specific behavior and its circuitry (e.g., freezing in the face of an uncertain danger) with an emotion category (e.g., *fear*). The problem with this logic is that it limits the definition of a complex psychological category to one or two behaviors. If *fear* is defined by freezing, then is *fear* not occurring at times when a rat flees, attacks, kicks bedding at a predator, or avoids an unknown corner of a maze? Or when humans avoid a dark alley, bungee jump, remember the events of September 11th, lock the door at night, or password-protect their bank accounts? As each of these actions is associated with a different neural network, which one is the *fear* network? If they are all fear networks, then what is the scientific value of the category *fear* for explaining behavior?

If discrete emotion categories are not associated with a specific brain locale, or even an anatomically inspired network that can be inherited, it is still possible that a pattern classification analysis on our meta-analytic database might reveal that each emotion category is represented by a specific combination of brain regions that co-activate together in time as a functional unit. We did not test this hypothesis, although we are in the process of developing these techniques for our software package. To the extent that such patterns are widely distributed across the brain, however (as opposed to being organized anatomically as inheritable units), such functionally defined networks for emotion categories (i.e., networks that only combine in a given context to produce a given type of mental state) would be consistent with a psychological constructionist (as opposed to a locationist) view.

It is possible that we failed to find evidence for the brain basis of discrete emotions because the methods employed in neuroimaging studies (or the laboratory for that matter) do not reliably elicit the type of discrete emotion experiences observed in the real world. After all, many scientists believe that emotions involve action (or action tendencies), and during scanning experiments participants must lie very still. Although this always remains a possibility, we do not believe it is a serious concern. First of all, even when participants are asked to lie still in a scanner, we still routinely observe increases in PAG activity in emotion. The PAG is necessary for motivated action patterns in animals, so these findings argue against the criticism that emotions invoked in the scanner are superficial. Even studies in which people are asked to imagine an emotional scenario probably create real experiences (as anyone knows who has become immersed in a mental reverie).

Finally, and perhaps most importantly, our observation that common brain activations exist across emotion categories is echoed in the pattern of findings for other (non-brain) measures of emotion. Since the beginning of psychology, researchers have questioned the idea that discrete emotion categories are each associated with a single, diagnostic pattern of response in the brain and body (e.g.,

Duffy 1934; Hunt 1941; James 1884; for a review of such theories, see Gendron & Barrett 2009). More recently, a number of empirical reviews (Barrett 2006a; Barrett et al. 2007a; Mauss & Robinson 2009; Ortony & Turner 1990; Russell 2003) have highlighted the disconfirming evidence: Different discrete emotion categories are not distinguished by distinct patterns of peripheral physiology (Cacioppo et al. 2000; Mauss & Robinson 2009), facial muscle movements (Cacioppo et al. 2000; Russell, Bachorowski & Fernandez-Dols 2003), vocal acoustics (Bachorowski & Owren 1995; Barrett 2006a; Russell, Bachorowski & Fernandez-Dols 2003) or by subcortical circuits in the mammalian brain (Barrett 2006a; Barrett et al. 2007a). The present meta-analytic review adds to this literature by demonstrating that emotion categories do not map to discrete brain locales in the human brain either. Instead, evidence from our meta-analysis, as well as studies of emotion that use psychophysiological measures, objective measures of the face and voice, and subjective experience of emotion, all point to the idea that emotions emerge from a set of more basic operations (cf. Barrett 2006b). As neuroscientific methodologies progress, it will become increasingly important for scientists to formulate a viable conceptual framework for mapping emotions to the brain. Our findings suggest that a psychological constructionist approach might offer just such a framework. Locationist views might be deeply entrenched in commonsense, which makes the corresponding scientific models particularly compelling, but they do not match the scientific evidence in any measurement domain for emotion.

6.2. Future directions in the search for the brain basis of emotion

Despite the field's emphasis on locationist views (that inspired many of the experiments used in our meta-analysis), we found that the bulk of the empirical evidence is more consistent with the hypothesis that emotions emerge from the interplay of more basic psychological operations. We hypothesize that these operations and their corresponding neural networks influence and constrain one another to produce a variety of brain states that correspond to a variety of emotional states. To fully explore the power of a psychological constructionist approach in future research, researchers might combine traditional neuroimaging techniques with methods that make more network-based assumptions about brain function (e.g., Multivoxel Pattern Analysis: Haxby et al. 2001; Multivariate Partial Least Squares Analysis: McIntosh et al. 1996) (see Schienle & Schafer [2009] for additional analysis approaches). Researchers might also utilize resting state analysis to identify functional networks that are intrinsic to the brain and compare those to the task-related assemblies of brain areas found across neuroimaging experiments (e.g., Smith et al. 2009). Finally, researchers must employ studies that capture and model the variability inherent in the collection of instances that form an emotion category like *anger*, *disgust*, *fear*, and so forth (e.g., Wilson-Mendenhall et al. 2011). Most studies in our database utilize stimuli and induction techniques that invoke the most typical – and even caricatured – instances of an emotion category. Yet, daily experience tells us that there is great variability in the instances of *anger*, *disgust*, *fear*, *happiness* and *sadness* that we experience, and research bears this out. For example, an instance of *disgust* that occurs when watching others eat repulsive food involves a different brain state than an instance of *disgust* that occurs when watching surgical operations (Harrison et al. 2010). Brain states that occur during instances of *fear* and *anger* are best described by an interaction between the content of the experience (e.g., whether the state is labeled *fear* vs. *anger*) and the context in which it occurred (e.g., a physical vs. social context) (Wilson-Mendenhall et al. 2011).

7. Unifying the mind

A psychological constructionist approach is not only a viable approach for understanding the brain basis of emotion, but it might also offer a new psychological ontology for a neuroscientific approach to understanding the mind. If a psychological constructionist approach to the mind is correct, then some of psychology's time-honored folk distinctions become phenomenological distinctions. This has implications for understanding a range of psychological phenomena, including decision making, attention, visual perception, mental illness, and perhaps even consciousness more generally. Indeed, similar efforts are emerging in other psychological domains (Fuster 2006; Poldrack et al. 2009; Price & Friston 2005; Warnick et al. 2010). According to a psychological constructionist view of the mind, *emotion* does not influence *cognition* during decision-making as one pool ball exerts influence on another. Instead the view suggests that core affect, conceptualization, and executive attention (and perhaps other psychological operations) cooperate to realize a behavioral outcome. If this is the case, then we might not assume that *emotion* and *cognition* battle it out in the brain when a person makes the moral decision to sacrifice one life to save many (e.g., Greene et al. 2004), or that consumer decisions are predicated on competing affective and rational representations (e.g., Knutson et al. 2007). Instead, we might assume that affect and executive attention are merely different sources of attention in the brain, rather than processes that differ in kind (Barrett 2009b; Vuilleumier & Driver 2007). Feeling and seeing might not be as distinct as is typically assumed (Barrett & Bar 2009; Duncan & Barrett 2007). Even conceptions about "internal" versus "external" processing begin to break down when we take into account the fact that "internal" ingredients such as affect and conceptualization shape the very way in which exteroceptive sensory input is realized as perceptions by the brain (Bar 2009; Barrett & Bar 2009). A psychological constructionist framework of the mind thus begins to break down the most steadfast assumptions of our commonsense categories. In so doing, it charts a different but exciting path forward for the science of the mind.

SUPPLEMENTARY MATERIALS

Figure S1: http://www.journals.cambridge.org/bbs2012008
Figure S2: http://www.journals.cambridge.org/bbs2012008
Figure S3: http://www.journals.cambridge.org/bbs2012008
Figure S4: http://www.journals.cambridge.org/bbs2012008
Table S1: http://www.journals.cambridge.org/bbs2012008
Table S2: http://www.journals.cambridge.org/bbs2012008

Table S3: http://www.journals.cambridge.org/bbs2012008
Table S4: http://www.journals.cambridge.org/bbs2012008
Table S5: http://www.journals.cambridge.org/bbs2012008
Table S6: http://www.journals.cambridge.org/bbs2012008
Reference for supplementary material:
http://www.journals.cambridge.org/bbs2012009

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NOTES

1. These hypotheses have been inspired, in large part, by behavioral neuroscience research in nonhuman animals that has carefully mapped the circuitry for behavioral adaptations that occur in response to specific environmental challenges (e.g., freezing, attack, vocalizations). One variant of a locationist view focuses on the circuitry for behavioral adaptations such as freezing, escaping, aggressing, and so on (e.g., LeDoux 2007; Panksepp 1998), and assumes that one behavioral adaptation is at the core of each discrete emotion category. However, this one-to-one correspondence between a behavioral adaptation and a discrete emotion category has been challenged on the basis of existing research showing that mammals such as rats display a variety of behaviors based on what is most effective in a given context (for discussion, Barrett 2009a; Barrett et al. 2007a).

2. For example, because the neurons within the amygdala are part of the neural reference space for discrete emotion, we can say with some certainly that the amygdala is likely to have increased activation when a person is experiencing or perceiving any emotion. This does not mean that the amygdala is necessary to each and every instance of emotion or even that it is specific to emotion, however. These ideas distinguish our approach from locationist accounts that assume that neurons within a given brain area (e.g., the amygdala) are consistently and specifically linked to a particular category of mental state (e.g., "fear").

3. Here we use the term "functionally selective" to mean that a brain area can have some preference for certain mental states, even if it is not specific to that mental state. Functional selectivity might occur because a brain area supports a more basic psychological operation that helps to construct a certain mental state (e.g., the amygdala supports detection of salient exteroceptive sensations and is functionally selective for instances of *fear*). Functional selectivity does not refer to specificity, however. A brain area might be functionally selective for one mental state or even one basic psychological operation in one instance, and another state or operation in another instance. Functional selectivity is distinct from the concept of "selective influence" (cf. Sternberg 2001), where a brain area being involved in one mental state (e.g., an instance of *fear*) but not another (e.g., an instance of *anger*) is taken as evidence of modularity.

4. For example, given that there is an increase in activation in the amygdala, the probability that a person is experiencing fear might be 0.7. The probability that he or she is experiencing another emotion (e.g., anger, disgust, happiness or sadness) is $1 - 0.7 = 0.3$. The odds ratio $= 0.7/0.3 = 2.33$. This means that given increased amygdala activation, the odds are 2.33 to 1 that the person is experiencing fear. In this case, the experience of fear is 113% more likely to predict increased activation in the amygdala than any other emotion state.

5. These findings might explain the amgydala's role in "fear learning" without assuming that the amygdala is specific to fear. In "fear learning," for example, amygdala activity reflects orienting responses that occur when an organism learns to associate a neutral stimulus with an already salient stimulus. The amygdala contributes to the production of the skin conductance responses (SCRs) (Laine et al. 2009) used to index "fear learning." Amygdala responses are associated with SCRs that occur immediately following the onset of a conditioned stimulus, suggesting that the amygdala is particularly involved in attention during learning but perhaps not the formation of associations (Cheng et al. 2007; also see Blakeslee [1979] and Spinks et al. [1985] for evidence that SCRs covary with changes in attention). This orienting account would also explain why increased amygdala activity is observed when animals learn to associate neutral stimuli with rewarding outcomes (e.g., Paton et al. 2006; for a review see Murray 2007), why amygdala activity corresponds to evaluative goals in the presence of both positive and negative stimuli (e.g., Cunningham et al. 2008; Paton et al. 2006), and why stimulation of the amygdala facilitates orienting responses such as startle (Rosen & Davis 1988). Together, these findings make it clear why the amygdala is so ubiquitously involved in mammalian social behavior (i.e., male and female sexual behavior, maternal behavior, aggression; see Newman 1999).

6. More than 90% (53/57) of study contrasts assessing *fear* perception in our database used startled faces that are unfamiliar to college students (who are typically participants in neuroimaging studies of healthy samples) (Whalen et al. 2001) and are highly arousing (e.g., Russell & Bullock 1986). Approximately 35% (15/43) of study contrasts assessing the experience of *disgust* presented participants with images that were novel (i.e., infrequently experienced in the industrialized world) and highly arousing (i.e., containing contamination, mutilated body parts, maggots, etc.).

7. EEG findings do not associate instances of *anger* with OFC specifically, probably because EEG does not easily pick up activity in the orbital sector.

8. The medial OFC (mOFC) and the sACC, which are more generally part of VMPFC, were part of the neural reference space and are reported in separate sections. Aspects of VMPFC that do not include mOFC/sACC were part of the neural reference space, but were not significant at the thresholds we report in this article.

9. In some theoretical treatments of emotion, emotion regulation is thought to be a separate psychological event from emotion generation, with distinctive neural correlates; in a psychological constructionist approach, however, the processes are the same because there is no conceptual distinction between generation and regulation (Gross & Barrett 2011).

10. "Resting state" or "default" networks are evidenced as correlations between low-frequency signals in fMRI data that are recorded when there is no external stimulus or task. These networks are thought to be intrinsic in the human brain. For a review of intrinsic networks and their function, see Deco et al. (2011).

Open Peer Commentary

Prime elements of subjectively experienced feelings and desires: Imaging the emotional cocktail

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Abstract: Primary affects exist at an ecological-communicative level of analysis, and therefore are not identifiable with specific brain regions. The constructionist view favored in the target article, that emotions emerge from "more basic psychological processes," does not specify the nature of these processes. These more basic processes may actually involve specific neurochemical systems, that is, primary motivational-emotional systems (primes), associated with specific feelings and desires that combine to form the "cocktail" of experienced emotion.

Lindquist et al. offer an outstanding compilation, organization, and presentation of the results of human neuroimaging studies related to emotion. Their study is of great interest as a review and summary of empirical data from this burgeoning area of research. The interpretation of these data, however, is flawed. It criticizes a so-called locationist model that specific brain regions are consistently associated with specific emotion categories, and reports little evidence for such associations. However, no one holds the simplistic view of brain–emotion relationships illustrated in the target article's Figure 1. It is a "straw man." Views such as those of Panksepp (1998) linking specific emotion categories with brain networks are not inconsistent with the pattern of results summarized in this article. Indeed, the pattern illustrated in Figure 3 of the target article supports the classic view of the brain and emotion dating from Papez (1937) and MacLean (1993): richly interconnected limbic structures associated with subjective emotional experience, and connected with many other brain areas. Indeed, the differentiation of core limbic, lateral limbic, and medial prefrontal cortex (PFC) subsystems in Figure 3 is not unlike MacLean's differentiation of subcortical-reptilian, selfish-paleomammalian, and prosocial-paleomammalian subsystems.

The quest to find specific brain locations associated with the primary affects – happiness, sadness, fear, anger, and disgust – is off the mark because the primary affects exist at an ecological rather than a bio/physiological level of analysis (Buck 1984; 2010). They are properly measured at the level of communication – display and pre-attunement – as they traditionally have been in research on facial displays.

The favored alternative "psychological constructionist" view assumes that emotions "emerge out of more basic psychological operations that are not specific to emotion" (target article, sect. 3, para. 1). However, the nature of these mechanisms is unclear. The notion of core affect, that all affect can be reduced to dimensions of valence and arousal, is not helpful.

However, the conclusion that emotions emerge from more basic processes may be on the mark. There *are* specific neurochemical systems underlying primary motivational-emotional systems or primes (Buck 1985; 1999). These include neurotransmitter molecules and receptors that vary in number and sensitivity. The activation of many primes is associated with specific, subjectively experienced feelings and desires, as demonstrated by the effects of psychoactive drugs on animals, including humans (Buck 1999). Many such transmitter molecules are peptides, direct products of genes in sending neurons. Specific peptides are associated with specific subjectively experienced feelings and desires (Pert 1997), and as the origin of the peptides is the genes, subjectively experienced affects function as "voices of the genes." The genes are always murmuring and whispering, generating a complex background of feelings and desires, but like the feel of our shoes on our feet, we rarely pay attention. Of course, sometimes the genes scream and shout, and our feelings and desires dominate consciousness. The genes do not control us through these feelings and desires, but they do cajole us.

Primes constitute modules, as it were, which, although dissociable in principle, are highly interactive, and combine to contribute to complex subjective experiences such as those associated with primary affects. For example, the subjective experience associated with fear might be composed of a variable neurochemical "cocktail" that might combine diazepam-binding inhibitor (DBI: the "anxiety peptide"), corticotrophin-releasing hormone (CRH: stress), cholecystokinin (CCK: panic), among others (Buck 2010). Similarly, love is arguably a primary affect at the ecological level, associated with intimate displays (contact comfort, pheromones). The subjective experiences associated with love may be associated with a neurochemical cocktail including high endorphins (euphoria), gonadotropin-releasing hormone (GnRH: eroticism), dopamine (DA: excitement), oxytocin (OXY: nurturance); vasopressin (AVP: protectiveness), CRH (stress); and low serotonin (5-HT: submission) (see Ortigue et al. 2010; Panksepp 1998). Understanding of these systems, their evolutionary and genetic bases, their complex interrelationships, and their communicative role in social interaction is proceeding apace.

Therefore, the contention that emotion requires a constructionist account may be accurate, but it is a neurochemical, biomolecular construction: arguably, "cocktail" is a better term. Also, this version of the locationist position is squarely on the mark: specifiable neurochemical systems, or primes, are constituent elements of the affective cocktail.

There is a 500-pound gorilla lurking largely unacknowledged in this article, and more generally in the literature on the brain and emotion: that is, cerebral lateralization. Right- and left-sided brain mechanisms are distinguished in the presentation of the empirical results of Lindquist et al., and there are many such differences, including an apparently larger neural reference space associated with emotions in the right than in the left hemisphere in the ventral view in their Figure 4. However, there is little discussion of the meaning of these differences. The discussion of the amygdalae and fear does not note evidence of amygdala lateralization, including sex differences. Whereas the right amygdala has been particularly associated with fear, there are suggestions that the left amygdala may be involved in socio-emotional functioning. There is evidence of left amygdala hypoactivation in Asperger Syndrome (AS: Ashwin et al. 2007) and hyperactivation in Borderline Personality Disorder (BPD: Donegan et al. 2003; Koenigsberg et al. 2009). Although these conditions have, historically, rarely been compared with one another, the evidence that they are related to the same brain area highlights the fact that in many ways their symptoms are opposite. Major AS symptoms include an obliviousness to other persons: a lack of empathy and socio-emotional reciprocity, and a preference for solitary activities. In contrast, BPD involves a kind of socio-emotional hypervigilance, often including frantic efforts to avoid real or imagined separation, rejection, or abandonment. These findings are in turn consistent with the observed sex differences: males tend to be emotionally oblivious and females emotionally hypervigilant. Hence, "the battle of the sexes."

This evidence, that the left amygdala is involved in the functioning of what might be termed a "social brain," is consistent with suggestions that the left hemisphere is associated with prosocial emotions (Buck 2002; Ross et al. 1994). The evidence in the target article, that anger experience is often associated with left-sided processing, is not inconsistent with this, as anger often functions as a prosocial emotion.

Understanding emotion: Lessons from anxiety

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Abstract: We agree that conceptualisation is key in understanding the brain basis of emotion. We argue that by conflating facial emotion recognition with subjective emotion experience, Lindquist et al. understate the importance of biological predisposition in emotion. We use examples from the anxiety disorders to illustrate the distinction between these two phenomena, emphasising the importance of both emotional hardware and contextual learning.

Lindquist et al.'s meta-analysis convincingly disproves the strong locationist account of the brain basis of emotion. Yet, one needs look no further than the myriad different presentations of anxiety disorders to see that the experience of emotions such as fear is highly idiosyncratic. As behaviour originates in the brain, this idiosyncrasy must be reflected at the neural level, and we endorse Lindquist et al.'s emphasis on context and prior learning in shaping emotional experience. This process, referred to by Lindquist et al. as *conceptualisation*, has been described extensively in cognitive models of psychiatric disorder in terms of schema (e.g., Beck & Emery 1985). However, the universality of facial emotion recognition and the cross-cultural ubiquity of anxiety disorders, suggest that emotional hardware is more important than Lindquist et al. suggest.

We agree that the basic emotions as described by Lindquist et al. are unlikely to represent the most basic psychological emotional processes in the brain. However, by combining facial emotion recognition with subjective emotion experience, Lindquist et al. understate the importance of biological hardware in facial recognition. There is strong evidence that facial expressions are universal social signals, and reading emotion expressions in others is conserved across cultures (Ekman 1973), albeit with some cultural constraints (Elfenbein & Ambady 2002). Evidence suggests that humans are biologically prepared for facial expression recognition. Infants aged 5–7 months can reliably distinguish between most facial emotion expressions, and are beginning to show adult-like attentional preferences for threat emotions such as fear (for review, see Leppänen & Nelson 2009). Around this age infants also show increased startle responses to acoustic probes in the presence of angry, relative to happy, faces (Balaban 1995).

Research by Schofield et al. (2007) replicated by ourselves (i.e., Button et al., unpublished results) has found that social anxiety is not associated with differences in recognising facial expressions but is associated with differences in attributions of personal cost to those same expressions. Similar results have been found across anxiety disorders; emotion recognition does not vary as a function of anxiety, whereas other processes, such as attention, are selectively enhanced for threat emotions such as anger (for review, see Bar-Haim et al. 2007). These findings suggest that facial expression recognition is relatively robust to the influences of anxiety schema. Furthermore, they illustrate how different patterns of neural responses may arise during simple face emotion viewing tasks due to processes such as attribution and attention.

The universality of the clinical syndrome of anxiety disorders (e.g., Horwath & Weissman 2000) suggests that emotional hardware is also important in subjective emotion experience. Vulnerability to anxiety disorders is heritable (Hettema et al. 2001). Evidence that non-phobic individuals report as many aversive experiences with a fear-stimulus as do individuals who are phobic of that stimulus (Ehlers et al. 1994; Merckelbach et al. 1992) suggests that factors other than contextual learning are important in fear responses. However, compared to the relative robustness of facial emotion recognition, subjective emotions are strongly influenced by anxiety schema, as they have the broader function of guiding perceptions of, and responses to, the environment (Cosmides & Tooby 2000; Damasio 1996).

Variations in the physiological responses which characterise different anxiety disorders provide evidence for the influence of anxiety schema on subjective emotion experience. Specific phobias are characterised by relatively normal baseline autonomic activity, with strong elevations in autonomic activity in the presence of the phobic situation (e.g., Hofmann et al. 1995). This pattern of activation is consistent with the specificity of the phobic schema (e.g., spider fears) to the phobic stimulus (e.g., spiders).

By contrast, generalised anxiety and generalised social anxiety are associated with elaborate schemas involving excessive worry about worry and fears of social ridicule and rejection, respectively. As such, a much wider array of stimuli and ruminative thoughts can trigger anxiety, which is reflected in a generally elevated baseline arousal observed in the hypothalamic–pituitary–adrenal axis and sympathetic adrenal medullary activation (for review, see Craske 2003). This increased baseline arousal is associated with a hypervigilance for threat. However, responses to acute stressors in generalised anxiety do not reliably differ from controls, and chronic worriers actually show reduced variability in heart rate and skin conductance during psychological stress (Hoehnsaric et al. 1989; 1995).

McNeil et al. (1993) found that shame and embarrassment result in decreased cardiovascular activity, suggesting that during times of social fear the parasympathetic shame response competes with the sympathetic fearful response, resulting in an attenuated heart rate increases in persons with social phobias. These conflicting processes of shame and fear are likely to be reflected in patterns of brain activity, illustrating the complexity of subjective emotion experience.

Recognising facial expressions is highly conserved, and the influence of anxiety schema on this process is relatively subtle. By contrast, the experience of anxiety and fear is highly idiosyncratic, reflecting much greater influence of contextual learning and belief systems, referred to as *schema*. Given the idiosyncrasy of fear experiences, reflected in the diversity of physiological responses outlined above, we agree with Lindquist et al. that subjective emotional experience is likely to be highly socially constructed. However, the evidence does not support Lindquist et al.'s claim for the social construction of basic emotion recognition, suggesting instead that humans are biologically prepared for facial expression recognition.

The strong locationist model cannot account for the differences observed in emotion recognition and subjective experience. Neither can it account for the idiosyncrasy of emotional experience. We agree with Lindquist et al. on the need to identify the basic psychological processes underpinning emotion. However, in attempting to encompass all the complexity of human emotion into a single model, the result lacks predictive value. If we accept that subjective emotion is socially constructed, then models which address the question of what emotions are and how they are represented in the brain are unhelpful. A more fruitful approach to establishing the brain basis of emotion (and cognition in general) is perhaps to ask what a given brain region does, and why.

Overcoming the emotion experience/expression dichotomy

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Abstract: We challenge the classic experience/expression dichotomous account of emotions, according to which experiencing and expressing an emotion are two independent processes. By endorsing Dewey's and Mead's accounts of emotions, and capitalizing upon recent empirical findings, we propose that expression is part of the emotional experience. This proposal partly challenges the purely constructivist approach endorsed by the authors of the target article.

An essential aspect of Lindquist et al.'s proposal in the target article concerns the attack on the classic attempt to functionally parcellate the brain, according to which, given a linguistically described mental process, a specific brain area underpinning it can be found. From the experimental point of view, the endorsement of such a "one word-one area" account of the mental domain has already shown its limits in the case of the classic cognitivist description of the mental processes underlying social cognition. According to this view, specific brain sites have been postulated to underpin the attribution of mental states to others by means of linguistic-like propositional attitudes, stimulating the search for a theory of mind reading brain modules. We do agree with the authors that such a transposition from language to brain sites could hinder our understanding of the brain, and we fully appreciate their view that words are "essence placeholders" (target article, sect. 3, see "Definitions"), helping to create categories in the absence of strong statistical regularities. The fact that different words designate different emotional states does not necessarily imply that such states can be directly mapped within specific brain locations.

Lindquist et al. frame this criticism within the locationist–constructionist debate, supporting the view that single emotions are not represented in specific brain regions, but rather are constituted by basic psychological operations common across different emotional domains. Despite the intriguing view they propose, however, the authors fail to describe what, according to a locationist approach, a cortical site for a given emotion is supposed to represent. This omission weakens the locationist approach, making it easier to criticize it. Consider the case of the insula. The authors claim that a locationist approach describes the insula as a region where disgust is processed; this view is then compared to a constructionist approach, according to which the insula is involved in "representing core affective feelings in awareness" (sect. 5.2., para. 2). Whereas the constructionist proposal is clearly explained, it is not as comprehensible what, according to the locationist approach, the insula is supposed to process ("perceiving instances of *disgust*," sect. 5.2., para. 1, italics in original).

In our view, this uncertainty is connected to the perspective that having an emotion is a "perceptual act" (see sect. 3, para. 2) during which the emotion "emerges in consciousness." According to the classic perspective the authors seem to endorse, experiencing a given emotion is similar to having a sensation, that is, it means feeling something. However, in their view, differently from sensations, emotions depend upon the "internal" world or, to use the authors' description, "core affect." It follows that experiencing and expressing a given emotion are two different and independent processes. The view that feeling emotions is a sensory activity, totally independent from their motor expression, is an old idea among scholars of emotions. In his seminal work, Darwin (1872) considered the emotion as a feeling preceding the emotional expression, whereas James (1884) considered the emotion as a feeling consequent to the emotional expression. In both cases, the motor output is not considered to be part of the emotion itself. The heritage of Darwin's and James's views strongly influenced contemporary neuroscientists, who mostly accept the experience/expression dichotomy, considering the emotional experience as a specific type of sensory activity (Craig 2002; Critchley et al. 2004; Damasio 1999). This perspective is clearly endorsed also by the authors of the target article.

An alternative perspective was offered, however, by Dewey (1894) and Mead (1895; 1934). Both Dewey and Mead explicitly criticized the experience/expression dichotomy by stressing the lack of any proof of the previous existence of the emotions with respect to the emotional response. In contrast, they suggested that the behavior connected to a specific emotion is part of the emotion itself. The sensory patterns directly trigger the motor representations associated with that specific emotion and this sensory–motor match *is* the emotion. The link between experience and expression has been partially recognized by recent neuroscientific studies. Botox injection in facial muscles decreases the strength of emotional experience (Davis et al. 2010). Activity in the left amygdala and in the brainstem is reduced during imitation of angry facial expression, if Botox is injected into the frown muscles (Hennenlotter et al. 2009). This effect likely reduces both the sensory input and the visceromotor output controlled by these structures. Even inducing the production of an emotional expression, or posture, enhances the correspondent emotional experience and influences the normal processing of the emotional information (Niedenthal 2007).

Even more dramatic is the case of the insula, described by Lindquist et al. as a region involved in the mental representation of bodily sensations. Recently, we showed that two different emotional behaviors can be evoked by the intracortical microstimulation (ICMS) of two different sectors of the macaque monkey insula (Caruana et al. 2011). ICMS of the anterior sector of the insula evokes a complex disgust-related behavior, characterized by a motor component (grimace of disgust) and a complex context-dependent behavior (refusal of food during stimulation). ICMS applied to a more posterior sector of the insula produces an affiliative behavior (lip-smacking).

Given the correlative nature of brain imaging, this approach hardly elucidates the possible causal role of a brain region in a specific emotional behavior. The choice of the authors to restrict their analysis only to neuroimaging, although done for practical reasons, weakens the result of their proposal. In fact, past electrophysiological studies showed that the stimulation of different emotion-related brain regions produces different behaviors related to specific emotions (for review, see Frijda 1986). It is not clear how a purely constructivist perspective could account for these data.

The locationist/constructionist debate could greatly benefit from overcoming the emotion experience/expression distinction, as has already happened in other fields of cognitive neuroscience, such as in the case of the perceptual experience of objects, space, and actions (see Gallese & Sinigaglia, in press). If a specific sensory pattern directly matches with a motor output (facial expression, visceromotor reaction), it makes sense to predict the existence of specific brain sensory-motor representations related to different emotional states. Is this locationist or constructivist?

A constructionist account of emotional disorders

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Abstract: Lindquist et al. present a strong case for a constructionist account of emotion. First, we elaborate on the ramifications that a constructionist account of emotions might have for psychiatric disorders with emotional disturbances as core elements. Second, we reflect on similarities between Lindquist et al.'s model and recent attempts at formulating psychiatric disorders as networks of causally related symptoms.

Fear is not localized in the amygdala, nor does sadness exclusively arise in the anterior cingulate cortex. Unfortunately for Gall (Gall & Spurzheim 1835), and more recent proponents, who hypothesized that single brain areas (later referred to as "particular circuits"; see Kandel & Squire 1992) correspond to single functions (e.g., arithmetic skills), feelings (e.g., pride) or attitudes (e.g., religiosity); *locationist* perspectives on such functions, feelings, and attitudes and their hypothesized unique "signature" in the brain increasingly turn out to be wrong (e.g., Bartholomew 2004; Poldrack 2006). Likewise, as Lindquist et al. convincingly argue, emotions are not recognized by the brain as separate entities and, as such, do not each have their own seat and unique activation signature in the brain. Instead, Lindquist et al. present a strong case for a *constructionist* perspective in which emotions are comprised of multiple, more basic processes, which are each associated with their own location and activation signature in the brain. The combined outcomes of these processes result in the individual experience of a particular emotion.

If Lindquist et al.'s constructionist perspective is an accurate representation of the relation between emotions and the brain, what ramifications might this have for those psychiatric disorders that have emotional disturbances as core elements? Among other processes, Lindquist et al. distinguish between *core affect* (i.e., mental representation of bodily representations) and *conceptualization* (i.e., sensations from the body or external world that are made meaningful). Major depression (MD) is a psychiatric disorder with "sadness" as one of the core elements, and it is well known that, in many cases, an episode of MD is preceded by stressful life events such as marital or health problems (e.g., Kendler et al. 1999). Although such life events are potentially quite aversive in nature, most people do not develop an episode of MD after experiencing them: So why are some people so severely affected by a stressful life event whereas most others are not? One explanation could be that in people who develop an episode of MD after a stressful life event the *conceptualization* process is dysfunctional; most people would respond with some sadness after a quarrel with a spouse (i.e., "normal" core affect), but in people with MD, this event is overly negatively conceptualized ("See, even my husband does not love me"). Such a hypothesis is consistent with clinical observations that patients with MD often engage in excessive rumination about past events (e.g., Roelofs et al. 2008a; 2008b).

On the other hand, in disorders with "fear" as a core element, the *core affect* process might have gone awry. Patients with a specific phobia are extremely fearful of certain objects (e.g., hypodermic needles), situations (e.g., flying an airplane), or animals (e.g., spiders) that do not elicit the same response in most other people. When confronted with, for example, a spider, patients with a phobia for that object will respond with various bodily sensations (e.g., profuse sweating, heart palpitations) to that object, whereas people without the phobia will not experience such bodily sensations; in terms of the Lindquist et al. perspective, specific phobia patients react with excessive *core affect* to phobic objects compared to non-phobic patients.

Distinguishing emotional disorders in terms of Lindquist et al.'s proposed processes might implicate a shift in clinical neuroscience from searching for *the* dysfunctional brain area causing a particular disorder to searching which brain areas do not *optimally work together* in perceiving and interpreting external stimuli (e.g., will we find that the conceptualization network is overly active in patients with MD?). This implication of Lindquist et al.'s work, that psychiatric disorders are not likely to be explained in terms of one dysfunctional brain area, bears a striking resemblance to recent attempts at formulating psychiatric disorders as networks of causally related symptoms (Borsboom 2008; Cramer et al. 2010; Kendler et al. 2011). In the *network approach*, psychiatric disorders are hypothesized to stem from direct interactions between symptoms (e.g., feeling tired → sleeping a lot → concentration problems) instead of from one underlying biological dysfunction (e.g., serotonin dysfunction causes all symptoms of MD). As such, each symptom is an autonomous causal entity and it is unlikely that such entities share the exact same etiological mechanisms: For example, symptoms such as insomnia and fatigue are likely governed by homeostatic processes, whereas symptoms such as guilty feelings and depressed mood are more likely regulated by cognitive processes (e.g., rumination). This hypothesis also lies at the heart of a theory in which psychiatric disorders are *mechanistic property clusters* (MPCs): mutually reinforcing networks of causal mechanisms at multiple levels of explanation (e.g., symptoms, brain). Each of these conceptualizations suggests that there are no hard delineations between disorders, as the processes that carry forward disturbances in a network are unlikely to be confined to a single set of symptoms (i.e., have a transdiagnostic character).

Thus, Lindquist et al.'s constructionist account is suggestive of mutually reinforcing networks at the brain level that, when working optimally, result in the subjective experience of an appropriate particular emotion (e.g., fear when confronted with an angry grizzly bear). However, if one or more of those networks do not optimally work together, the result can be an inappropriate emotion (e.g., excessive fear when confronted with a spider). Subsequently, the network approach (i.e., mutually reinforcing networks at the symptom level) explains why, for example, a dysfunctional core affect process does not result in a specific phobia but results in excessive fear of a particular object or situation: other symptoms of a specific phobia, for example avoiding the feared object or situation, are a result of the excessive fear (i.e., one symptom causing the other). One way to investigate this hypothesis is by gathering intensive time-series data with which one can accurately monitor the development of symptoms (and interactions among them) over time. This approach can be combined with frequent fMRI scans in order to link, for example, excessive activation of the conceptualization network, to the subsequent development of MD symptoms.

Emotions as mind organs

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Abstract: In matters of the mind, the opposition between what is mind-made or inside and natural or outside the mind is bound to misfire. Lindquist et al. build their analysis on a strong contrast between naturalism, which they reject, and psychologism, which they endorse. We challenge this opposition and indicate how adopting psychologism to combat a naturalistic view of emotional mind/brain areas is self-defeating. We briefly develop the alternative view of emotions as mental organs.

Lindquist et al. challenge the view that the most familiar emotion words and the linguistically expressed emotion experiences are ultimately the natural kinds found in the brain/mind, referred to as "naturalism" for short. Naturalism traditionally refers to the view that some of the entities the mind reasons with and decides about exist outside of and independent from these

mental operations. Let us label this physicalist naturalism. However, when naturalism is used to refer to putative entities in the mind/brain, the situation is much more complex. Mentalistic naturalism as opposed to physicalist naturalism, seems to postulate that there are entities in the mind that are not mind-made. As Lindquist et al. present it, for naturalism basic emotions are such mind-independent entities. Emotions, in the naturalistic view the authors challenge, stand for mind-independent or for biological categories, which are essentially present in the mind-brain. Psychologism, by contrast, does not build on anything given other than its own operations, which are the same whatever the subject matter.

Interestingly, the description of the alternative view Lindquist et al. endorse, psychological constructivism, consists of entirely content-general mental operations that operate over inputs that are not necessarily emotional. So, other aspects aside, the contrast the authors set up is between emotional determinism and emotional indeterminism of the mind's building blocks.

The inherent contradictions of an area-focused meta-analysis. Lindquist et al. are rightfully critical of the approach that has been prominent in the majority of brain imaging studies aspiring to localize the neurofunctional basis of each single emotion in a dedicated brain area. For example, the amygdala was the fear area, the insula was the disgust area, and so forth. Meta-analyses inherit the weak points of still less-than-perfect brain imaging techniques and cannot but endorse and amplify them. fMRI studies vary widely in scanner properties, in settings, in designs, and in tasks, including the involvement of attention, awareness, and contrast stimuli or conditions. The meta-analysis exploits the very procedures under attack by using positive activation levels of isolated brain areas themselves obtained in a wide variety of studies. The meta-analytic conclusion that some areas play or do not play their anticipated role, does not invalidate their role, and this role may or may not show up in fMRI analysis. For example, the amygdala was repeatedly shown to play a role in processing of emotional stimuli, and brain imaging studies of autism are consistent with this. However, patients with Urbach-Wiethe syndrome have a major deficit of the basolateral amygdala, yet show no signs of autistic behavior. There are many more examples illustrating that there is no rigid link between a brain area and a functional deficit. But the suggestion of attributing functions to a network rather that to a single area is likely to beg the question. Another approach to emotions is needed. It must be possible to avoid naive naturalism and extreme psychologism.

Emotions are mind organs. Emotions are mind/body adaptations, evolved in natural and social contexts (in a partly species-specific way). As emotions serve different goals, they have evolved next to each other and inhabit brain/body resources in different ways to fit their goals (Panksepp 1998). Yet in contrast to many approaches, different emotions are interdependent and interrelated. We do not believe that emotions must await neuroanatomical dissection to prove that they operate as cooperating distinct entities, even if functional distinctions can be made and appear in clinical symptoms. We know that this is unrealistic with current functional neuroimaging techniques. For example, different emotions produce different facial expressions in a predictable way, although we can reasonably assume that we are unable at the moment to distinguish between motor activity associated with angry versus fearful expressions. In the very same way, the visceral activation and the associated feeling will be different between disgust and anger, but it is unlikely that these emotional experiences can be disentangled spatially by their cortical somatosensory responses. In our view, emotions entail a distributed neural system, and focusing on its components, whether from a locationist or from a psychological constructionist perspective, is equally and inherently reductionist. First, psychological constructivism reduces emotions to a sum of parts, ignoring that a particular neural component exerts its function in relation to and sometimes driven by the other components of the individual emotion system (e.g., Benuzzi et al. 2009; Liang et al. 2009). This emotion-specific connectivity pattern is an essential and mandatory characteristic of emotions. Second, by attributing a specific psychological operation to a gross anatomical component, the degrees of freedom of the functional contribution of this component to a particular emotional state are reduced. For example, the amygdala may signal motivational salience in some instances but may critically contribute to the fear response in others. Patients with epilepsy caused by sclerosis of the amygdala, for example, may experience intense fear during their seizures, in the absence of any relevant object (Van Paesschen et al. 2001). Third, emotion-specific activation at the cellular level in monkey studies (Kuraoka & Nakamura 2007) somewhat contradicts the postulation of generic regional operations that is made by psychological constructivism.

Just as organs have different functions in the body, emotions serve different functions in the mind. The traditional terminology of basic emotions as states is indeed inappropriate to catch these functions. They encompass not just a network of brain areas, as these activation peaks are the tip of the iceberg. Beneath the neurofunctional facts revealed by brain imaging studies of neurotypical subjects, are structural facts, inhibitory and excitatory modulations in dynamic networks, endocrinological signatures, behavioral engrams laid down by phylogenetic and ontogenetic experience, and so on. Most importantly in this context, the function of an organ, in this case the minds' emotions, needs to be understood in relation to the others and of the whole. Just as the body cannot be reduced to a collection of independent organs, the emotions operate in concert, and whether in health or in sickness, they need to be considered together. Balanced or unbalanced, the interaction between the emotion organs makes and breaks the self. One may still call this "psychologism," but then any view on emotions is "psychologism."

A rigorous approach for testing the constructionist hypotheses of brain function

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Abstract: Although the target article provides strong evidence against the locationist view, evidence for the constructionist view is inconclusive, because co-activation of brain regions does not necessarily imply connectivity between them. We propose a rigorous approach wherein connectivity between co-activated regions is first modeled using exploratory Granger causality, and then confirmed using dynamic causal modeling or Bayesian modeling.

Lindquist et al. seek to distinguish between locationist and constructionist models of emotion by performing a meta-analysis of brain activations during various types of emotional stimuli. Methodologically speaking, the discovery of activated brain areas using the general linear model is primarily geared towards the

locationist framework because it is a univariate method, which assumes that each voxel time series is independent of others. However, interaction between voxel time series from different brain regions is imperative for the constructionist model to work. Consequently, any evidence for the constructionist model from an analysis of activations is tenuous and indirect. Therefore, in our opinion, although this target article provides strong evidence against the locationist view, the evidence for the constructionist view is not conclusive. The authors do offer the future possibility of pattern classification of the meta-analytic database showing associations between emotional category and a set of co-activated brain regions. This might be a step forward, but it still does not directly model the interactions between brain regions.

Here we present a rigorous approach for testing the constructionist view. If a set of brain regions co-activate in response to an external stimulus of emotional value, then there must be significant information transfer between the co-activated regions. For example, a fearful stimulus may first activate the sensory regions, which transmit that information to the amygdala, which determines the stimulus to be motivationally salient. The insula may encode the visceral reaction to it and then transmit it to the orbitofrontal cortex. The visceral information from the insula, the salience information from the amygdala, and executive attention from the dorsolateral prefrontal cortex, may all converge in the orbitofrontal cortex (or some other prefrontal area) and be integrated to create the experience of fear (or any other emotion). The constructionist hypothesis predicts that different regions encode some basic psychological operations, which, when integrated, "feels" like different emotions. In the aforementioned example, the co-activation of a set of brain regions is only a necessary condition for the constructionist view, but is not sufficient. Only a model which can capture and quantify the task-associated connectivity between regions can provide sufficient evidence for the constructionist hypothesis. We will now describe how such models could be used for directly testing the constructionist hypothesis.

Granger causality analysis (GCA) is based on the principle that if the past activity of region A can predict the present and future activity of region B, then A must have a causal influence on B. Traditionally, GC is obtained from the vector autoregressive model wherein GC from time series j to time series i is given by the ijth element of coefficient matrix (Deshpande et al. 2009). GCA is completely data-driven, accommodating a large number of time series in the model, and is primarily an exploratory technique. Many refinements to GCA have been proposed, such as correlation-purged/dynamic/nonlinear GC (Deshpande et al. 2010; Marinazzo et al. 2008; Sato et al. 2006) and hemodynamic deconvolution (Havlicek et al. 2011; Ryali et al. 2011), which have increased the applicability of GCA to fMRI. On the other hand, dynamic causal modeling relies on modeling underlying neuronal causality using state-space equations and Bayesian inference for comparing model evidence. Although dynamic causal modeling is restricted by the number of time series (up to 8), it is a robust confirmatory technique. We propose combined use of GCA and dynamic causal modeling for testing the constructionist hypothesis. First, GCA could be employed on time series from a large number of nodes, similar to the number used in the target article, provided there are enough subjects for such an analysis to be adequately powered. Using an iterative network reduction procedure we have previously proposed (Deshpande et al. 2008), the large exploratory network could be reduced to a smaller network by removing network redundancies, which could then be confirmed by either dynamic causal modeling (if the reduced network has fewer than 8 nodes) or other methods such as Patel's tau (τ) (Sathian et al. 2011), which are not based on autoregressive principles but rather on Bayesian inference. In this way, converging evidence can be obtained from multiple and distinct methodologies for quantifying the magnitude and direction of connectivity between co-activated brain regions. Such an analysis could provide sufficient evidence for the constructionist hypothesis.

In section 6.1 of the target article, paragraph 2, the authors suggest that studies of resting states will be useful in determining if there are "intrinsic" functional networks corresponding to emotion categories or basic psychological operations underlying them. Here we address some pertinent methodological advances in fMRI research in this direction. While most neuroimaging studies of resting state networks have concentrated on functional connectivity based on instantaneous correlation (which is a non-directional influence) in a single network, we investigated both functional connectivity and effective connectivity (which is a directional influence) of four different resting state networks using a single multivariate model (Deshpande et al. 2011). This enabled an explanation of the basic psychological operations during the resting state, such as episodic memory, self-referential processing, and cognitive integration in terms of significant pathways in the network. We believe that this study will provide significant insights for testing the constructionist hypothesis using resting-state data.

Emotional participation in musical and non-musical behaviors

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Abstract: Existence of similarities of overall brain activation, specifically during emotional and other common psychological operations (discussed by Lindquist et al.), supports a proposal that emotion participates continuously in dynamic adjustment of behavior. The proposed participation can clarify the relationship of emotion to musical experience. Music, in turn, can help explore such participation.

Lindquist et al.'s data analysis in the target article can support continuous rather than episodic involvement of emotion in "mental engagement" (Gardiner 2008c), my terminology for the functional action of the brain that generates behavior.

Study of the emotional components of musical experience (Gardiner 2003; 2008b; Juslin & Vastfjall 2008) can help to develop our understanding of emotional participation in mental engagement, once we enlarge theoretical orientation towards musical evidence. Juslin and Vastfjall and others search for specific features within heard music that evoke emotion. But to account for much of the richness, variety, and subtlety of emotion within musical experience (Dewey 1934/1980), we should view emotion as most generally generated by integral participation in, rather than response to, music.

Emotion (Damasio 1999) is related to an adjustment of body physiology and brain activation and restoration that maintains overall homeostatic equilibrium while also addressing the behavioral needs of an organism. Body and brain activities are marshaled for fleeing, fighting, or pursuing a mate, with restoration taking place during relaxation and rest. But activation and restoration must be addressed and balanced throughout every behavioral state, as the recovery of every nerve after firing illustrates. At least in humans, conscious awareness concerning emotion (Damasio 1999) must have a role as well. Emotion and feeling reflect (James & Lange 1922) and influence (Cannon 1929) adjustments of body and brain physiology, but the details of how this occurs are still not fully resolved.

Emotions include not only primary emotions of happiness, sadness, fear, anger, surprise, and disgust (Damasio 1999), but also social emotions such as embarrassment, jealousy, guilt, and

pride, and background emotions such as well-being, malaise, calm, and tension. Emotion and feeling thus concern not just shorter term physiological adjustments, but also have influence on longer term adjustments of behavior. Variety, mixtures, and fluctuation of experienced states can frustrate verbal classification, but normal experience shows no breaks in emotion and feeling.

Detection of specific sensory stimuli signaling a critical need for action can trigger almost immediate emotional response (Damasio 1999; LeDoux 1996), but, especially in humans, emotional reaction to most stimuli depends greatly on context.

Consider now the calm, peace, and admiration of beauty one can experience while walking quietly through a beautiful forest. Similar emotional components can be experienced during what Dewey terms the musical experience (Dewey 1934/1980), produced as one progresses at a slow rhythmical-walking ("andante") pace through listening to music at the beginning of the "andante" of Mozart's Piano Sonata K.V. 283, while admiring its beauty, or still more, if one is able to move easily through the activity of playing this music while conscious of its beauty.

Here, similarity in sensory stimuli reaching one during these non-musical and musical activities cannot account for any similarity of experienced emotion. But both the non-musical and musical activities involve progression through activity at a similar rhythmic and "andante" rate to which body and brain may well make similar physiological adjustment. Both activities involve awareness of and emotional reaction to the enjoyment of beauty. And both may well involve emotion registering and interacting with the ease and lack of impediment with which behavior progresses. As this example illustrates, the involvement of emotion in non-musical behaviors can help us understand its involvement in musical behaviors as well.

The growing evidence relating emotion to adjustment of physiology to maintain homeostasis (Damasio 1999) should direct us towards further developing our understanding of connections between details of mental engagement and emotion. Every act of mental engagement, whether it produces motor behavior or not, depends upon and may well also affect physiology of brain and body. I propose that accumulating evidence implies that much of mental engagement involves interaction within complexes that incorporate interconnected levels of engagement (see also, Chase & Simon 1973; DeGroot 1965). Higher-order motor acts, such as the utterance of a verbal phrase or the playing of a melodic phrase, are built from lower-level motor acts that generate the utterances of phonemes, or the playing of individual musical notes. Listening acts involving speech or music are as much acts of mental engagement as are acts that produce motor consequences such as talking or singing. The dynamic structure of these acts of composite engagement make continuous demands on brain and body physiology. If indeed emotion is intimately related to adjustment to demands on physiology, as work for more than a century implies, then it would be very useful for humans and other creatures to have evolved not only the large-scale emotion-related adjustments that are already increasingly well understood, but also as deep an involvement of emotion-related detailed physiological adjustment interacting with mental engagement at all its levels, about which far less is known so far. The influence on and interaction with emotion plausibly comes, I propose, at every level of the mental engagement that compositely generates behavior – this including the highest levels of engagement that generate coordinated activity over significant periods of time, such as, in the example discussed, walking through a forest, or playing a piece of music (see also Clynes 1977).

Detailed involvement of emotion at all levels of mental engagement is of course extremely difficult to explore. Here I believe that music in its rich connection to emotional experience can give us many important windows of opportunity. As an example, consider the extent to which seemingly subtle changes in music can lead to striking shifts from positive to negative emotional experiences. The positive emotions experienced while engaged in listening to or playing the beginning of the Mozart Piano Sonata K.V. 283 andante written in the key of C Major can shift immediately to negative emotions of brooding sadness if one plays this music, or listens to it played, instead in the key of C Minor, even if all other features of the performance remain unchanged. The musical change involves only a small difference in certain critical musical notes, in particular every E lowered to E flat. An opposite effect can be demonstrated with the opening of the Mozart Piano Sonata K.V. 310 in A Minor, where the experience of intense grief – related, I suspect, to the death of Mozart's mother – is immediately changed to a sense of triumph and exhilaration if the piece is played in A Major. I trace such differences in emotion to differences in the musical scales, which affect tensions and their release within melodies and associated harmonies, major scales promoting a sense of forward and upward movement, and minor ones pushing rather down and against forward movement. Negative emotions such as sadness or grief may then reflect, in part, the sense of continuous obstruction to movement that the music illustrates.

Humanity may well have developed music (see Gardiner 2000; 2003; 2008a; 2008b; 2008c; Gardner et al. 1996) to produce experiences that further exploited to its own benefit its evolved capabilities for mental engagement importantly including engagement involving emotion. We should continue to use our musical creations to further study ourselves.

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What can neuroimaging meta-analyses really tell us about the nature of emotion?

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Abstract: In Vytal and Hamann (2010) we reported a neuroimaging meta-analysis that found that basic emotions can be distinguished by their brain activation correlates, in marked contrast to Lindquist et al.'s conclusions in the target article. Here, I discuss implications of these findings for understanding emotion, outline limitations of using meta-analyses and neuroimaging as the sole basis for deciding between emotion views, and suggest that these views are essentially compatible and could be adapted and combined into an integrated emotion framework.

Lindquist et al. present an innovative answer to the question of how the human brain generates emotions, in the form of their conceptual act model (CAM). This model combines embodied cognition, psychological construction, and other approaches into an impressive and sweeping theoretical framework, which provides a fascinating counterpoint to more established models. The CAM offers a fresh perspective and will surely generate much-needed debate and discussion that will foster new theoretical development and empirical studies in this area.

I would like to distinguish here between the merits of the CAM and the particular meta-analytic approach taken to demonstrate support for it in the target article. In this commentary, I focus on the latter and outline how our recent meta-analysis (Vytal & Hamann 2010), which found results supporting the basic emotion view, suggests important limitations for using meta-analyses as evidence to decide between emotion views. Next, I suggest that to properly evaluate different emotion views, neuroimaging evidence alone is not sufficient and needs to be supplemented by methods which can identify functionally essential regions. Finally, I suggest how these views, which are often

cast as incompatible, could potentially be combined into an integrated emotion framework.

Meta-analyses conflict over support for basic emotions. Our meta-analysis, using a different but related method (Laird et al. 2005), supported the conclusion that basic emotions have consistent and discriminable (specific) brain correlates (Vytal & Hamann 2010). These findings, summarized in Figure 1 of this commentary, showed that each pair of basic emotions (e.g., *happiness* vs. *fear*) could be distinguished by differences in regional brain activation likelihood (see Vytal & Hamann 2010 for details). In marked contrast, Lindquist et al.'s meta-analysis found *no* evidence for specificity.

What are the implications of these discordant findings? One implication is that results of meta-analyses can be strongly influenced by initial assumptions, analysis choices, and decision criteria, and that caution should be taken when relying on only one approach. For example, to address specificity, we used a standard approach to establish discrimination ability by statistically contrasting activation maps for each possible pair of emotions. In their most comparable analysis, Lindquist et al. used a different but equally acceptable approach, contrasting individual emotions with the average of all other emotions. These different decision criteria will necessarily lead to different conclusions in some cases. Although the authors include other analyses, these derive from the same density analysis. The fact that different meta-analyses that use standard methods can lead to opposite conclusions suggests that it may be premature to conclude that CAM is supported by neuroimaging meta-analysis.

Different criteria and definitions complicate comparison of views. Beyond the issue of meta-analysis methods lies another basic problem for comparing emotion views: widely differing criteria. The criteria for supporting basic emotions are strict and highly specific, whereas those for CAM are lenient and very flexible. The authors acknowledge these issues and take steps to counter this bias where possible. Critically, however, no evidence is provided to confirm that these steps are actually effective. Without such evidence, it would again seem premature to draw firm conclusions.

A related issue concerns how basic emotion (locationist) views are defined. The target article focuses exclusively on testing the most limited version: single brain regions uniquely associated with specific basic emotions. However, the recent literature suggests that most neuroimaging researchers acknowledge that emotions arise from networks of two or more regions. For example, amygdala activity increases along with increasing emotional arousal across a wide range of emotions, both pleasant and unpleasant (Hamann et al. 2002).

Given this well-known counterevidence, it seems unlikely that most well-informed neuroimaging researchers would contend that the amygdala is *only* responsive to fear, or that amygdala activation would not be associated with other emotions. The fact that Lindquist et al.'s conclusions do not apply to basic emotion views that postulate network implementations significantly limits the scope of the target article's conclusions, relative to current debates. Indeed, the target article leaves open the possibility that basic emotions may be based on brain networks.

Considering converging evidence from other methods is essential. A final consideration is that neuroimaging can only establish associations between emotions and regions of brain activation, not whether these regions are functionally essential for an emotion as opposed to being inessential, merely co-activated regions. Because the focus of the emotion debate is on the

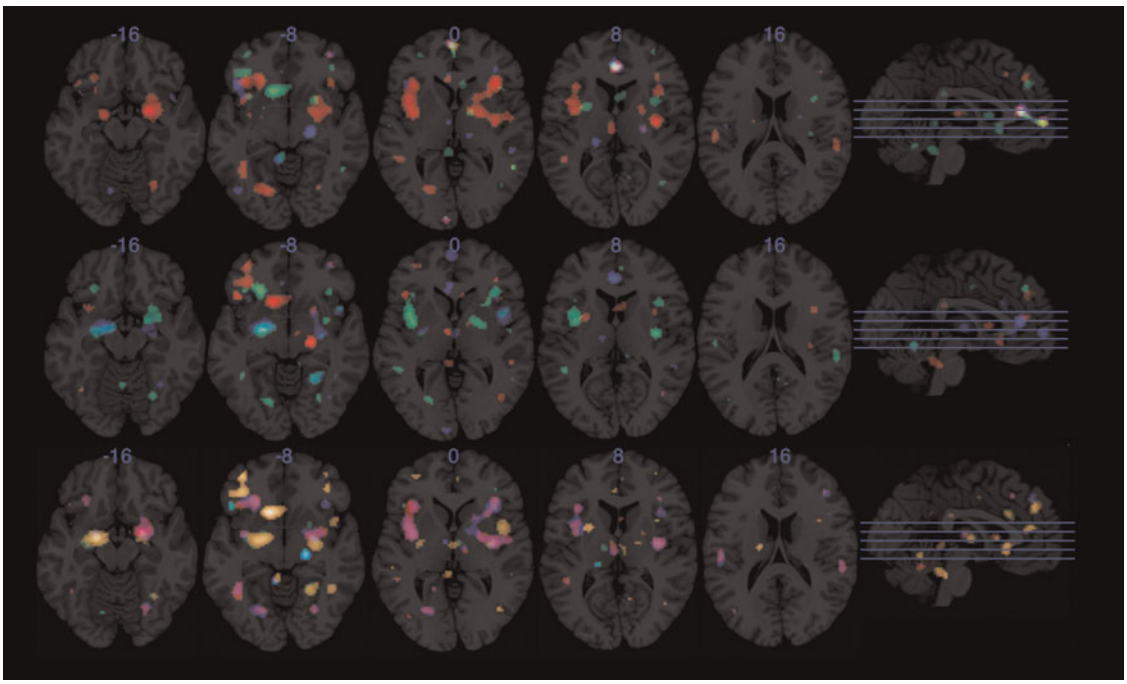

Figure 1 (Hamann). Summary of brain regions whose activity discriminated between each pair of basic emotions in our previous meta-analysis. (Results adapted from Vytal & Hamann 2010.) Each colored region shows brain regions where a direct statistical meta-analytic contrast of activation likelihood significantly distinguished between pairs of basic emotions. Colors are superimposed on a standard anatomical MRI brain image in Montreal Neurological Institute (MNI) space, with the right of the images showing the right hemisphere. Blue numbers indicate inferior-superior level (z). Where colors overlap they combine additively; for example, red and blue overlap to equal purple). For clarity, the 10 pairwise contrasts are displayed in three separate groupings. **Top panel:** Red: happiness vs. disgust; Green: happiness vs. sadness; Blue: happiness vs. anger. **Middle panel:** Red: sadness vs. anger; Green: fear vs. disgust; Blue: fear vs. happiness. **Lower panel:** Red: sadness vs. disgust; Green: fear vs. anger; Blue: anger vs. disgust; Gold: fear vs. sadness. A color version of this image can be viewed in the online version of this target article at http://www.journals.cambridge.org/bbs.

brain processes *essential* for generating emotions, it follows that to properly evaluate the evidence for different emotion views, it will be critical to consider converging evidence from methods that can establish whether brain regions are functionally essential for emotion. Such methods include studies of patients with brain lesions, and stimulation methods such as intracranial brain stimulation.

Summary. The foregoing points suggest that Lindquist et al.'s meta-analysis has some important limitations. These limitations raise concerns about interpreting the meta-analysis conclusions as supporting the CAM and as constituting evidence against basic emotion views. The two emotion views in the target article have been frequently cast as mutually incompatible, competing views. However, an alternative approach might be to explore how elements of both views can be combined, creating a hybrid view that would combine key advantages of both. A synthesis seems possible. If Lindquist et al.'s meta-analysis had supported the existence of one basic emotion, for example, *fear*, it is likely that this could be accommodated within the flexible CAM. If core affect is proposed to be an inborn ability "given by nature" (Barrett et al. 2007a), and core affect may evolve to include other distinctions such as approach/avoidance, it is conceivable that other distinctions, perhaps some resembling basic emotions, could be encompassed within core affect.

In conclusion, the highlights of this thoughtful and intriguing article are its elaboration of the CAM and its discussion of neural mechanisms of emotion. The CAM is an important contribution to longstanding debates on the nature of emotion, independent of potential concerns about supporting evidence in the target article. The interplay between such models and other views will help spark the evolution of new neuroscientific theories about how the human brain generates emotions.

Psychological constructionism and cultural neuroscience

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Abstract: Lindquist et al. argue that emotional categories do not map onto distinct regions within the brain, but rather, arise from basic psychological processes, including conceptualization, executive attention, and core affect. Here, we use examples from cultural neuroscience to argue that psychological constructionism, not locationism, captures the essential role of emotion in the social and cultural brain.

Strikingly, several regions reviewed by Lindquist et al. are not only involved in the perception and experience of emotions, but are the very same neural regions most often implicated in social behaviors. Here, we argue that culture as the broadest form of social behavior depends upon – and evolved along with – general neural mechanisms underlying emotion. Specifically, we use cultural neuroscience findings on emotional vigilance and empathy to illustrate that general mechanisms, rather than specific emotional modules, support how we think, feel, and behave in our social worlds.

Implicating the basic processes of executive attention and core affect in social contexts, cultural neuroscience research reveals a relationship between collectivism and emotional vigilance. Specifically, participants primed with collectivistic values responded more quickly to fear-relevant stimuli in a dot-probe task (Chiao & Lee 2011). This is further supported by a cross-cultural study of Japanese, Japanese-American, and Caucasian-American participants, demonstrating that Japanese, relative to Americans of either race, show heightened amygdala activity in response to negative emotional stimuli (Chiao et al. 2011). Furthermore, bicultural Asian-Americans primed with collectivistic values show increased amygdala response to negative emotional stimuli, indicating that being in either an individualistic or collectivistic cultural mindset elicits a culturally congruent emotional effect (Hechtman et al. 2011).

We interpret these findings as suggesting that collectivism necessitates increased emotional vigilance (in a constructionist's framework, core affect and executive attention). For example, collectivistic nations have historically had higher levels of environmental threat, such as increased pathogen prevalence, which may require vigilance for survival (Fincher et al. 2008). Furthermore, collectivistic cultures typically place a strong emphasis on group membership and hierarchy (Fincher et al. 2008). These tight constraints on appropriate social behavior may require increased attention to negative cues in one's environment, in order to correct one's behavior and bring behavior into line with social norms. Building on this evolutionary perspective, genetic factors may parallel and support culture's influence on emotion. For instance, recent evidence suggests that the serotonin transporter gene (5-HTTLPR) – known to regulate neurotransmission within the amygdala and other regions supporting emotional vigilance (Munafo et al. 2008) – may have co-evolved along with cultural values of individualism–collectivism (Chiao & Blizinsky 2010). Specifically, collectivistic nations have larger proportions of individuals who carry the S compared to the L allele of the 5-HTTLPR (Chiao & Blizinsky 2010). S-allele carriers show increased amygdala response to negative stimuli (Hariri et al. 2002), paralleling the cultural effects. We therefore propose that genetic and cultural factors have exerted mutual evolutionary influence on neural systems underlying attention and core affect.

As implied by this culture-gene coevolutionary view, the aforementioned findings on amygdala and associated genes can be interpreted as mechanisms tuning people's basic emotional processes. This is consistent with a view of the amygdala as not merely supporting a discrete emotion category, but as a center that modulates other regions to create a nonspecific state of emotional vigilance (Davis & Whalen 2001). Similarly, since the amygdala typically serves an important social function (Adolphs 2010), its activity likely enables appropriate cultural behaviors based on environmental context. Altogether, the amygdala functions as a modulator of emotional and attentional processes. A locationist view of emotion therefore fails to account for how the brain evolved and how it carries out its responses to sociocultural and environmental demands.

Besides moderating emotional vigilance, culture shapes other social cognitive processes involving core affect and conceptualization. Particularly, culture influences neural mechanisms underlying group coordination and helping behaviors, such as empathy and pro-sociality (Boyd & Richerson 2009). When empathizing with others' feelings, people recruit the bilateral insula, the anterior cingulate cortex (ACC), and somatosensory cortices during both perception and experience of others' emotional states (Lamm et al. 2011). Additionally, neural response is enhanced within brain regions associated with mentalizing, such as the medial prefrontal cortex, which likely reflects the recruitment of self-related processes for understanding and sharing the emotional states of others (Frith & Frith 2006).

Neural response within the empathic brain is modulated by a number of sociocultural factors, including social dominance orientation (SDO) (Chiao et al. 2009), implicit racial attitudes (IAT; Avenanti et al. 2010; Bruneau & Saxe 2010), racial identification (MEIM; Mathur et al. 2010), and modern racism (MR; Gutsell & Inzlicht, in press). Specifically, people with strong

social hierarchy preference (i.e., high SDO) show less ACC and insula activity when empathizing with others' pain. Additionally, people with stronger racial IAT biases show reduced sensorimotor response to out-group members (Avenanti et al. 2010). Beyond ACC and insula activity, MEIM predicts extraordinary in-group empathy in African-Americans, indexed by increased activity in the medial prefrontal cortex (MPFC) (Mathur et al. 2010). Furthermore, MEIM is associated with default-mode network activity within cortical midline structures (Mathur et al., in press). Finally, Gutsell and Inzlicht (in press) demonstrate the association between MR and prefrontal asymmetry.

Similar to the proposed roles of the amygdala, neural mechanisms underlying empathy can be interpreted from an evolutionary perspective. In constructionist terms, processes of core affect (e.g., in the ACC and insula) and conceptualization (e.g., in the MPFC) give rise to empathy, which channels people's emotion towards others through re-experience of their feelings. Empathic processes, then, may have evolved to support prosocial behaviors in groups and, in turn, may have coevolved with intricate sociocultural structures. For example, sociocultural constraints on empathic feeling (e.g., SDO, racial IAT, MEIM, and MR) likely create (and are enabled by) differential feelings for others based on group and/or status. Here the modulation of various processes (e.g., core affect and conceptualization) supports both differential feelings towards, and differential concepts about, other people. Localist views of emotion cannot account for the multiple converging, socially shaped processes crucially involved in empathic feeling.

In sum, using cultural neuroscience work on emotional vigilance and empathy, we illustrate that both social and emotional behaviors are products of basic processes that are culturally and environmentally shaped. This process view, assuming evolutionary development of fundamental psychological building blocks, accounts for the vast overlap in social and emotional brain regions. Together, cultural neuroscience research, accounting for the evolution of culturally appropriate forms of emotion, supports constructionist, but not localist, views on emotion.

Further routes to psychological constructionism

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Abstract: In this commentary, we do two things. First, we sketch two further routes to psychological constructionism. They are complementary to Lindquist et al.'s meta-analyses and have potential to add new evidence. Second, we look at a challenging kind of case for constructionism, namely, emotional anomalies where there are correlated, and probably relevant, brain anomalies. Psychopaths are our example.

Lindquist et al. demonstrate that there is little evidence for a locationist approach to emotion. We, too, think that the evidence points toward psychological constructionism, the view that emotions of a certain kind are constructed out of more general brain structures whose function is not specific to emotions of that kind, or even to emotions at all. There is not much evidence that emotions are localized in specific, unique regions of the brain dedicated to a particular kind of emotion alone and no other cognitive function. There is even less evidence for the modularity that has often accompanied the localization hypothesis.

This commentary aims to add two things. First, we suggest that there are other routes to the same constructionist conclusion. We sketch two. They are complementary to the meta-analyses of Lindquist et al. and have the potential to add a considerable amount of new evidence. Second, we look at what is perhaps the most challenging type of case for constructionism, namely, the existence of emotional anomalies where there is evidence for specific, highly correlated, and probably relevant brain anomalies. We have chosen psychopaths as our example.

One additional route to evidence concerning constructionism would be to look at "task specifics," that is, the specifics of the context of individual occurrences of a kind of emotion. Consider anger. Anger can be produced by many input modes: seeing, hearing, recalling, being told. Some situations leading to anger are more difficult to understand than others (i.e., they impose a greater cognitive load; Lindquist et al. touch on this issue in section 5.4, para. 4). At the output end, the manner in which anger is expressed varies enormously from case to case, especially across cultures, genders, and socio-economic groups (Ekman 1993; Cheng et al. 2005). Sometimes anger expresses itself in physical aggression, sometimes in verbal aggression, sometimes in contempt (of which there are in turn many forms), sometimes in passivity, sometimes in deliberately blunted affect ("coldness"). (Lindquist et al. touch on this as well [sect. 6.1, para. 3], but do nothing with the observation. Indeed, it is not even clear whether for them expression is part of emotion.) Therefore, our question is: Since these different ways of expressing anger are almost certainly associated with widely different regions in the brain, are there any regions or sub-regions activated throughout the different kinds and contexts of anger? If no region or sub-region is activated across all the differences of input, cognitive demand, and output, that would be important further evidence for constructionism.

One could use task specifics in a number of other ways. For example, one could look at cases where expression is roughly constant across occurrences but underlain by very different emotions. Or one could try to factor out differences in brain activation associated with different reasons for a given kind of emotion, or differences resulting from personality type or psychological disorder.

Another way to generate data relevant to constructionism would be to look at cases in which a stimulus generates a judgment about an emotion rather than the emotion itself; for example, where a face is interpreted as expressing anger but does not make the subject feel angry. In the relatively unemotional judgment about the stimulus, are the same areas activated as when the subject actually feels angry?

In the same vein, there are cases where we would expect a face to be interpreted as expressing anger, but some subjects interpret it instead as expressing pain. Would the same areas be activated as when subjects interpreted faces in line with our expectations as expressing anger? And what about activation associated with differences of experimental protocol (reaction time or decoding, masking or no masking, variations in the emotional intensity of the stimulus, and/or differences among different kinds of stimulus set, visual modality [seeing vs. hearing], and level of cognitive load)? The research questions behind task specific studies are: (1) Concerning a given emotion, what are the activation patterns for different patterns of vision, cognition, and expression? And, (2) Do these patterns lend any support to the localization hypothesis?

Psychopaths, in whom striking emotional anomalies are strongly correlated with specific brain anomalies, appear to challenge constructionism. The emotional anomalies associated with psychopathy include callousness or lack of empathy, lack of remorse and guilt, and shallow affect (Cleckley 1982; Hare 1991). Turning to task specifics, psychopaths often react differently from non-psychopaths to emotionally laden stimuli. The emotional anomalies in psychopaths are usually specific to fear (Blair et al. 2001). They show little startle reaction in fear situations (Patrick et al. 1993) and poor decoding of fearful facial expressions (Blair et al. 2004) in comparison to non-psychopaths.

They also present with a distorted ability to allocate attention in a way that reflects the emotional content of stimuli (Lorenz & Newman 2002; Newman et al. 2010). (The latter already points to constructionism.)

What about the underlying, correlated brain activation? While the anomalies suggest amygdala dysfunction and there is indeed evidence for this (Blair 2005; 2008), the behavioral evidence strongly supports constructionism – indeed, more than Lindquist et al. fully recognize. They associate the psychopath's aggression with anger (sect. 5.3, para. 1). In fact, there is far more variability in psychopaths than this. In psychopaths, aggression tends to play an instrumental role as opposed to the reactive role that it usually plays in non-psychopaths (Hart & Hare 1996). Aggression appears to be how psychopaths respond to a wide variety of situations about which they have a wide variety of feelings. If this is true, aggression in them is likely to be associated with a wide range of emotions, not just anger. This conclusion supports constructionism.

Thus, not only does psychopathy not threaten psychological constructionism, it offers support for the view. We expect that the same will be true for other syndromes that have seemed to some to offer evidence for localization.

Scaffolding emotions and evolving language

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Abstract: We suggest that, in animals, the core-affect system is linked to partially assimilated behavioral dispositions that act as developmental scaffolds for the ontogenetic construction of emotions. We also propose that in humans the evolution of language altered the control of emotions, leading to categories that can be adequately captured only by emotion-words.

We are in sympathy with the constructionist view of emotions put forward in the target article, "The brain basis of emotion: A meta-analytic review." The results of Lindquist et al.'s meta-analysis are consistent with other comparative imaging studies, and with what is known about the inherently plastic exploration–stabilization processes that occur in the nervous system during development and learning. More generally, the results are in line with the growing evidence that commonalities at high levels of organization are underlain by variable networks that have only family resemblance with each other: The components of the networks provide *facilitating* rather than necessary or sufficient conditions for macro-level properties. We want to suggest two ways in which the authors' interpretation of the data can be supplemented. First, we suggest adding to their model a factor that helps to explain what Barrett (2006b) has called the "emotion paradox" – the discrepancy between the perceived similarity that subjects and observers find among instances of "basic emotions" and the extreme variability among the neural and physiological correlates of such instances. Second, we expand on the role of language in the construction of human emotional categories.

We think that Lindquist et al.'s model does not provide a full solution to the emotional paradox. The analogy with color categories, which are also constructed categories, is not convincing because the biological affordances in this visual system – *specific* receptors for different wavelengths – do not have a counterpart in the model the authors describe. We believe that such a counterpart does exist, and that it is what James referred to as "instinct": evolved behavioral dispositions, which, when the behavior they drive is first elicited, are the *developmental scaffolds* for constructing habitual motor behaviors and emotions (James 1890/1950, Ch. 24). We regard Jamesian "instincts" as partially genetically assimilated behavioral dispositions that evolved in ways that make their typical behavioral manifestations require relatively little (initial) learning.

Examples in mammals are freezing, appetitive behavior, and so on. In normal animals such behaviors, *as they are practiced*, are constituted by specific coordinated motor reactions that have feedback relations with bound visceral sensations – with bodily experiences. In other words, initially, stereotypic behavior patterns inevitably have more or less stereotypic affective correlates – "first-time-feelings," which are, for example, the feelings that arise as a mouse freezes for the first time, or as a hen first sits on an egg (see James 1890/1950, Chs. 24 and 25). First-time feelings *are not* emotional categories, and, although similar, they are not identical among individuals of a species (because of the nature of early development). We think that they act as scaffolds for what, on the basis of ontogenetic experience and learning, later become a particular emotional category (e.g., freezing-fear). According to our view, an experienced, mature mouse has more than a general initial core affect; it has developmentally constructed emotional categories, although these categories are much narrower than those of humans, and are not adequately described in terms of human emotion-words (such as fear or love). They are better described in terms linked to the stereotypic responses, so a mouse might be said to have a freezing-emotion, or a maternal-care-emotion. These emotional categories are usually similar to but never identical to first-time feelings: The specific first-time feeling of freezing becomes enriched and fine-tuned during the ontogeny of each mouse as it interacts with predators (Ginsburg & Jablonka 2007a; 2007b; 2010a). In some cases the emotion associated with such scaffolds may be changed beyond recognition: for example, a male dog can be conditioned to react with an avoidance reaction to a bitch in heat (Gottlieb 1992), but in nonhuman animals this usually happens only under extreme or atypical conditions.

We therefore agree with Lindquist et al. that the emotions of nonhuman animals, like those of humans, are constructed during ontogeny from the stream of constantly evaluated homeostatic feelings (core-affect). These are what Lamarck called "inner feelings" (Lamarck 1809/1914, Book III, pp. 333–34), and we believe they appeared very early in the evolution of animals (Ginsburg & Jablonka 2010a; 2010b). However, we think that as the feelings that are the consequence of the activities occurring as "instinctive" responses are generated, they form one of the inputs that construct emotional categories. These initial affective dynamic states form only a developmental scaffold, but the "structures" built on this scaffold usually have sufficient family-resemblance to be recognized as belonging to a particular emotional category. Taking them into account renders the "emotion paradox" less paradoxical.

Although inborn predispositions may help in explaining the canalization of non-symbolically mediated *stereotypic* expressions of emotions, we share Lindquist et al.'s view that the tokens covered by *emotional categories constructed by language*, which include a very wide spectrum of behaviors and subjective states, may have very little in common with each other except for their symbolic references. We would like to expand on this point from an evolutionary point of view. The evolution of language, which led to the ability to communicate about the not-here and the not-now, engendered profound alterations in the emotional profile of humans. This was the consequence of, first, the expanding breadth of an individual's experiences brought about by sharing the experiences of others through linguistic communication; second, the accompanying development of personal autobiographies, which increased the coherence and specificity of individual experiences; third, the formation of social values and new social emotions; and fourth, the control (often the inhibition) of the affective triggers of action, of affect-related drives through linguistic communication.

Although the control of drives has ancient roots related to the evolution of episodic memory, tool use, and recall-for-planning, the human ability to communicate about the imagined necessitated an increase in this inhibitory capacity and in its regulation, and allowed the metaphorical transfer of symbols, creating new categories in all domains of human experience. All these led to emotional categories, which, as Lindquist et al. convincingly argue, are held together by emotion-words, and can be captured adequately only by symbols.

The sleeping brain and the neural basis of emotions

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Abstract: In addition to active wake, emotions are generated and experienced in a variety of functionally different states such as those of sleep, during which external stimulation and cognitive control are lacking. The neural basis of emotions can be specified by regarding the multitude of emotion-related brain states, as well as the distinct neuro- and psychodynamic stages (generation and regulation) of emotional experience.

According to the "conceptual act model," emotional experience is a result of a complex psychological operation termed "situated conceptualization," which gives a meaningful context to a basic core affect. Conceptualization is guided by fundamental cognitive processes such as retrieval of stored memory representations and executive attention. Accordingly, the neural basis of emotion processing is stated to be represented by a variety of interacting brain regions, which are traditionally associated with both basic psychological operations and emotional experience. In substantiating the role of conceptualization, the model accounts for the active states of the waking human brain, during which goal-directed behaviors induce a relevant context.

Critically, emotion categories can be generated during brain states which essentially differ from active wake in that goal-directed executive control networks are not active. Neuroimaging studies have demonstrated that brain areas including the dorsolateral prefrontal cortices (DLPFC), parietal cortices, precuneus, posterior cingulate cortex (PCC), and primary visual cortex, all of which support higher cognitive functions and executive control (Fuster 2006), are suppressed during rapid eye movement (REM) sleep compared with wake; whereas the anterior cingulate cortex (ACC), orbitofrontal cortex (OFC), amygdaloid complexes, pontine tegmentum, parahippocampal cortex, and extrastriate visual cortices are more active in REM sleep than in wake and non-REM sleep (Braun et al. 1997; 1998; Maquet et al. 1996; Nofzinger et al. 1997) (see our Figure1a). Yet, intensive emotional experience does exist during REM sleep, and the emotional categories of REM sleep do not differ from those experienced during wake (Fosse et al. 2004; Hobson et al. 2000; McNamara et al. 2010; Stickgold et al. 2001; Walker & van der Helm 2009). Importantly, in REM sleep, emotions emerge out of goal-directed behavioral context and under a lack of external input. Also, their conceptualization and goal-directed reference are elusive (Fosse et al. 2004; Hobson 1999; 2009; Hobson et al. 2000) as implied by the strong DLFC suppression during REM sleep.

In non-REM sleep, and particularly in slow wave sleep (SWS), the activity of all these brain areas is suppressed (Braun et al. 1997; Maquet et al. 1996; Nofzinger et al. 1997) and mental experience is extremely scarce (Hobson & Pace-Schott 2002). Nonetheless, although reports from non-REM sleep are often thought-like (Hobson 1999; Hobson et al. 2000), signs of emotions reflecting an individual's current concerns can be detected (Foulkes 1962; Hobson et al. 2000). Moreover, night terrors (*pavor nocturnos*) characterized by a general feeling of fear accompanied by intense autonomic discharge, typically occur during the deepest stage 4 of SWS (Gastaut & Broughton 1964; Gottesmann 2010). Thus, substantially different brain states such as those of wake, and non-REM and REM sleep – characterized also by dramatic differences in mentality, neurochemistry, connectivity, and neuroelectric signaling (Gottesmann 1999; Hobson & Pace-Schott 2002; Hobson et al. 2000; Stickgold et al. 2001; Tononi & Koch 2008) – can all provide a neural basis for the experience of distinct emotional categories. Further, in a variety of dysfunctional wake states associated with psychopathological and neurological deficits, sleep alterations (e.g., Benca et al. 1992) or sleep deprivation (Van der Helm et al. 2010; Yoo et al. 2007), in which critical brain regions and/or their connections are functionally altered (over-activated or de-activated), emotion generation is preserved, although subjective emotional experience can be modulated (Walker 2009).

State-related, in particular sleep-related, emotions can be viewed in the context of two existing concepts regarding the distinction between conscious and non-conscious processing of emotions, and the neurodynamics of emotional perception: (1) Increasing evidence is provided for the coexistence of two distinct neural systems in the waking brain, which subserve conscious and non-conscious processing of emotions (Morris et al. 1998; Vuilleumier et al. 2001). Non-conscious perception of emotional stimuli has been associated with the functional integrity of a subcortical network including the pulvinar, amygdala, nucleus accumbens, periaqueductal gray, and locus coeruleus (Morris et al. 1999; Tamietto & de Gelder 2010; Williams et al. 2006) (see our Figure 1b), which may function independently of cortical areas. It is proposed that this network incorporating also the ACC and OFC (Fig. 1b) is genetically established and phylogenetically adaptive, and can, through rapid feed-forward influences, enhance the pre-attentive processing of emotional signals during goal-directed behavior. It is only during wake that an executive cortical feedback is suggested to exert inhibitory modulation over emotion-related subcortical areas (Tamietto & de Gelder 2010). It is notable that major components of the non-conscious emotional system are overactivated during REM sleep relative to wake (ACC, OFC, and amygdala – see Fig. 1) implying enhanced emotion processing within this system due to the lack of inhibitory modulation from cognitive cortical areas. (2) Emotion perception is proposed to be underlain by three neurophysiological stages: (i) identification of emotional significance of information; (ii) production of affective state including the generation of autonomic, neuroendocrine, and neuromuscular responses and subjective responses of emotional experience; and (iii) regulation of the affective state (Phillips et al. 2003).

Within these concepts, physiological and subjective experience markers indicate that affective states are generated during sleep (Hobson & Pace-Schott 2002), but they are not regulated by cortical regions (Fig. 1). Emotion generation during sleep is entirely driven by internal information, being unaffected by operations subserving the interaction with the external environment (Hobson 1999). Thus, the emerging emotional categories may not be an online integrative product of ongoing context appraisal (as Lindquist et al. suggest in the target article). Rather, emotional dream experience reflects the functioning of local (Tononi & Koch 2008) or primary consciousness (protoconsciousness) defined as *simple awareness of perception and emotions* (Hobson 2009).

We argue that emotions emerge in a variety of distinct brain states. The neural mechanisms of emotion generation are different from the neural mechanisms of emotional regulation, with the latter

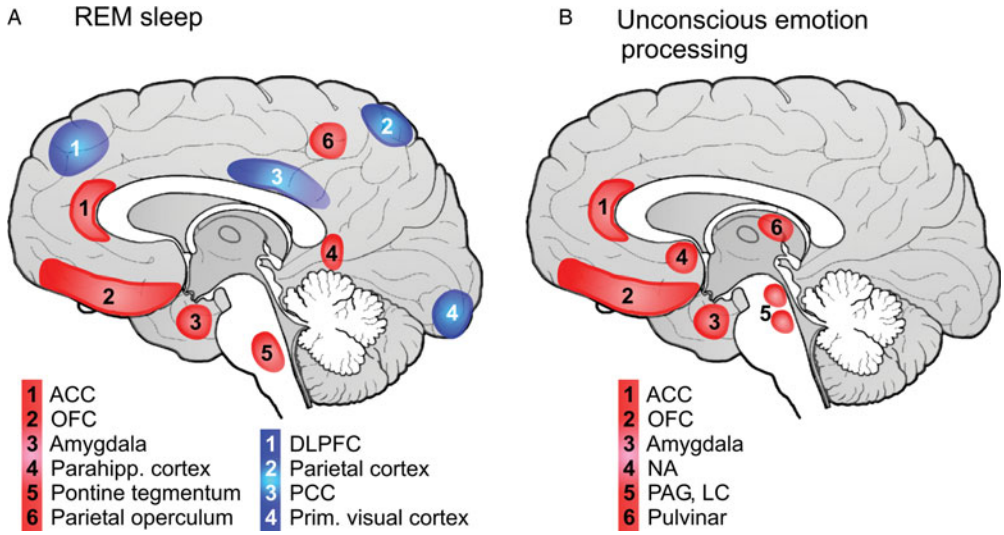

Figure 1 (Kirov). Regional activation patterns: (A) Blue (white numbers) and red (black numbers) areas indicate regions showing deactivation and hyperactivation, respectively, during REM sleep compared to wake (modification of Hobson 2009). (B) System of non-conscious emotion processing (modification of Tamietto & de Gelder 2010). ACC: anterior cingulate cortex; OFC: orbitofrontal cortex; Parahipp.: parahippocampal; DLPFC: dorsolateral prefrontal cortices; PCC: posterior cingulate cortex; Prim.: primary; NA: nucleus accumbens; PAG: periaqueductal gray; LC: locus coeruleus. A color version of this image can be viewed at http://www.journals.cambridge.org/bbs.

being able to modulate emotion production only during conscious processing. We suggest that the neural substrate of emotional categories can be identified adequately by exploring different functional brain states, in which emotion generation may not be dominated by the executive control mechanisms. Thus, models of the brain basis of emotion would demarcate the neural substrates of emotion generation, emotional experience, and emotional regulation.

Emotion and personality factors influence the neural response to emotional stimuli

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Abstract: Lindquist et al. assess the neural evidence for locationist versus psychological construction accounts of human emotion. A wealth of experimental and clinical investigations show that individual differences in emotion and personality influence emotion processing. These factors may also influence the brain's response to emotional stimuli. A synthesis of the relevant neuroimaging data must therefore take these factors into consideration.

Lindquist et al. address the long-standing debate concerning the representation of emotion at a neural level. They have used sophisticated meta-analytic techniques to determine the extent to which the brain honours locationist versus psychological constructionist accounts of emotion. Their analysis includes studies of emotion perception and experience that rely on a range of different stimuli, modalities, and cognitive processes, focusing on those studies that target discrete, or basic, emotions: anger, disgust, fear, sadness, and happiness. They conclude that the data show promise with respect to psychological construction accounts of emotion while providing little evidence for any consistent or specific correspondence between discrete emotion categories and distinct brain regions or networks.

The authors have contributed the largest meta-analysis of neuroimaging studies of emotion to date, and a psychological construction framework offers a valuable perspective on the affective neuroscience literature. In particular, it offers the potential for fruitful crossover with existing theoretical models in the cognition and emotion literature that emphasise the presence of multiple functional-level routes to the generation of emotion, such as schematic, propositional, analogical, and associative representational systems (SPAARS) (Power & Dalgleish 2008) and interacting cognitive subsystems (ICS) (Teasdale & Barnard 1993).

Nonetheless, we feel that despite the wealth of neuroimaging studies dedicated to delineating the brain basis of emotion, it is premature to conclude that particular brain areas do not have a preferential role in coding particular emotional attributes. Before accepting this position, alternative explanations for the absence of locationist evidence must receive careful consideration. Lindquist et al. raise several possibilities themselves – that functional neuroimaging has spatial and temporal limitations, that discrete emotion categories may be represented in networks (rather than specific brain regions) not identified by the current analyses, or that the methods used to target emotion in individual studies may not capture the full complexity or phenomenology of emotional processes and experience in real life. It should also be considered that rather than reflecting the absolute response within a network of regions, different emotional processes may depend on interactions (or changes in connectivity) between these regions.

To this, we would like to add that while neuroimaging can establish associations between activation of certain brain regions or networks and particular emotional or cognitive functions, it cannot establish the *necessity* of those brain regions for particular functions. Demonstration of the latter requires, for example, targeted neuropsychological studies of patients with sustained brain injury to focal neural regions. This perspective has significant implications for the interpretation of the neuroimaging data. Even where neuroimaging shows little specificity of function for a given brain region or network, it could still be the case that lesion studies support a locationist view by demonstrating that a given region is particularly important for one

emotion category. For this reason, neuroimaging evidence on its own cannot resolve this issue and must be considered in conjunction with corresponding human and animal lesion studies.

Finally, the vast majority of neuroimaging studies have studied neural responses to emotional stimuli in healthy individuals who are not preselected according to any specific criteria. However, there is tremendous variability in the extent to which healthy individuals vary in their experience of particular emotions or action tendencies, such as anxiety or behavioural activation. A wealth of cognitive and behavioural research has demonstrated that individual differences in relevant mood and personality dimensions influence the manner in which individuals process emotional stimuli. For example, behavioural studies in clinical and non-clinical populations show that individual differences in anxiety determine the behavioural response to emotional stimuli conveying threat (Bar-Haim et al. 2007).

Individual variation has received little consideration in the neuroimaging literature. However, it has been suggested that accounting for individual differences in relevant mood and personality dimensions may reveal aspects of neural function not readily apparent in studies that adopt standard group-based subtraction contrasts (Calder et al. 2011). To illustrate, functional neuroimaging studies have shown that anxiety levels in non-clinical populations correlate positively with the amygdala response to fearful faces, particularly when these stimuli are unattended or presented outside conscious awareness (Bishop et al. 2004). Moreover, although approximately 40% of studies in previous neuroimaging meta-analyses fail to find an amygdala response to fearful facial expressions (Murphy et al. 2003; Phan et al. 2002), a recent review showed that all studies investigating anxiety's influence on the brain response to fearful faces identified the amygdaloid area, regardless of whether the study showed an amygdala response (fear minus neutral contrast) across the entire group (Calder et al. 2011). Anxiety also influences the amygdala response to viewing facial signals of anger (Ewbank et al. 2010). Crucially, this effect is found only when angry faces are gazing towards, but not away from, the observer, suggesting that amygdala activity is not related to a specific facial expression but to the degree of perceived threat. A relationship has also been found between the ventral anterior insula response to pictures of disgusting foods and trait variation in disgust sensitivity (Calder et al. 2007).

These results do not necessitate that the amygdala or insula or, indeed, other regions, are associated with threat and disgust specifically. Rather, these regions may be associated with more abstract emotional attributes on which these emotions weigh heavily but not exclusively (Calder et al. 2007). To this extent, we do not disagree with Lindquist et al.'s conclusion that the brain may not respect discrete emotion categories per se. Nonetheless, we think it would be premature on the basis of neuroimaging data alone to say that the amygdala, for example, does not play a preferential role in coding a particular emotional attribute.

Studies such as those highlighted here suggest that the apparent inconsistencies observed in the literature may be attributable to variation in psychological dimensions that are meaningful and relevant to the particular emotion under consideration. The role played by these individual difference factors must therefore receive careful scrutiny and consideration before we can conclude that emotion categories are not natural kinds that are respected by the brain.

Emotions of "higher" cognition[1]

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Abstract: The target article by Lindquist et al. considers discrete emotions. This commentary argues that these are but a minor part of human emotional abilities, unifying us with animals. Uniquely human emotions are aesthetic emotions related to the need for the knowledge of "high" cognition, including emotions of the beautiful, cognitive dissonances, and musical emotions. This commentary touches on their cognitive functions and origins.

The target article by Lindquist et al. contributes a wealth of information to studies of emotions, and to psychology in general. However, I would expect such an in-depth article on emotions to address specifically human, "higher" cognitive emotions. Whereas in the past emotions were often considered irrelevant or opposite to cognition, recent research emphasizes closed relations between the two (Adolphs et al. 2002; Bechara & Damasio 2002; Bradley et al. 2001; Damasio 1995; Duncan & Barrett 2007; Grossberg & Levine 1987; Mayer et al. 2008; Ochsner & Phelps 2007; Perlovsky 2006c). Discrete emotions discussed in the article are limited in number and thus represent only a minor part of human emotional abilities. Specifically human emotions are related to "high" cognition. As discussed later, their number is very large, and this is why they are called "continuous." Musical emotions (Juslin & Västfjäll 2008) are an example of "continuous" emotions that set humans apart from the animal kingdom. Yet, the entire target article is devoted exclusively to discrete emotions that appear in the perception of concrete objects. Here are a few quotes from the article to support this point:

> "Emotions emerge when people make meaning out of sensory input from the body and from the world." (sect. 3, para. 2)
> "Emotions are 'situated conceptualizations'... because the emerging meaning is tailored to the immediate environment." (sect. 3, para. 2)
> "Core affect... is a term used to describe the mental representation of bodily changes." (sect. 3, para. 4)

These statements might almost equally refer to animals or humans. The target article does not consider emotions related to abstract concepts. No emotion of pleasure from understanding is discussed; for example, that understanding an object to be food might be emotionally pleasant for a hungry animal or human. But understanding is also pleasant in itself, otherwise there would be no motivation to understand abstract concepts. Understanding the meaning of one's life is emotionally pleasant; a simplified reason is that this is necessary for concentrating one's efforts on the most important goals. This emotion, according to Kant (1790), is related to emotions of the beautiful. Kant explained that aesthetic emotions are related to knowledge.

Specifically human "higher" cognitive emotions, especially musical emotions, have been called "mysterious" by thinkers from Aristotle to Darwin and by contemporary evolutionary psychologists (Aristotle 1995; Ball 2008; Darwin 1871; Masataka 2008). Yet, "higher" cognitive emotions have been studied by many authors. I will mention just a few references: emotions of cognitive dissonance (Cabanac et al., in press; Festinger 1957; Haidt 2001; Levine 2009; Levine & Perlovsky 2010; van Veen et al. 2009), musical emotions (Cross & Morley 2008; Juslin & Västfjäll 2008; Levitin 2006; Panksepp & Bernatzky 2002; Patel 2008; Perlovsky 2010d; 2010c; Purwins et al. 2008; Sloboda & Juslin 2001; Trainor 2008), and emotions of language prosody (Buchanan et al. 2000; Davis et al. 1996; Deacon 1989; Perlovsky 2006a; 2006b; 2009b).

Even when discussing emotions in voices, Lindquist et al. do not recognize them as possibly different from discrete emotions. Yet the voice of human languages carries a significant emotional load different from that of discrete emotions. Emotions in language sounds are similar to emotions in poetry and songs, and (among other things) motivate us to relate language sounds to their meanings (Perlovsky 2009b; 2010c). Animals relate sounds of voice to meanings automatically; in an animal's mind the sounds of voice are inseparable from the meanings. Humans have to be motivated to do this (Deacon 1989; Seyfarth & Cheney 2003a). Emotions related to knowledge of abstract concepts have been discussed

in Cacioppo et al. (1996), Levine and Perlovsky (2008; 2010), Perlovsky (2009b; 2010c), and Perlovsky et al. (2010), and emotions related to creativity discussed in Levine and Perlovsky (2010), Lubart and Getz (1997), and Pfenninger and Shubik (2001). "Emotions of the beautiful" are discussed in Biederman and Vessel (2006), Dorfman et al. (2006), Perlovsky (2002; 2006c; 2010b; 2010a), Tooby and Cosmides (2001), and in Silvia (2005). Yet the "beautiful" is mentioned only once in the target article: "A painting is beautiful" (sect. 3, para. 5). Emotions pertaining to the beautiful are not mentioned.

In the Perlovsky studies cited above, I have discussed evidence and other studies relating "emotions of the beautiful," as discussed by Kant, to the need for knowledge; aesthetic emotional mechanisms are essential in every act of perception and cognition; at the level of perception they are autonomous and below the threshold of consciousness, at "higher" levels of cognition they could be experienced as conscious emotions; they are in complicated interaction with cultural discussions of these emotions in language (which usually are more conscious). The origin of aesthetic emotional mechanisms is in the need to adapt mental representations to concrete conditions around us. Contradictions between basic drives and knowledge, as well as within the system of knowledge, cause emotions of cognitive dissonances. A need to resolve these contradictions emotionally is related to the origin of music. (These emotions are usually "continuous" because the number of contradictions, and therefore the number of emotions, is combinatorially large; Spinoza [1677/2005] was the first one to mention that emotions differ depending on the object of reference.)

Lindquist et al. mention in conclusion that emotions and cognition might be a unified process:

> [W]e might not assume that *emotion* and *cognition* battle it out in the brain . . . or that consumer decisions are predicated on competing affective and rational representations . . .. Instead, we might assume that affect and executive attention are merely different sources of attention in the brain . . .. Feeling and seeing might not be as distinct as is typically assumed. (target article, sect. 7, para. 1)

But no discussion was devoted to emotions related to cognition "above" perception of concrete objects. An opportunity to study specifically human "high" cognitive emotions has been lost.

NOTE

1. This is a work of the U.S. Government and is not subject to copyright protection in the United States.

Beyond brain regions: Network perspective of cognition–emotion interactions

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Abstract: Lindquist et al. provide a convincing case against what they call the *locationist* account of emotion. Their quantitative approach elegantly illustrates the shortcomings of this still-entrenched viewpoint. Here, I discuss how a network perspective will advance our understanding of structure-function mappings in general, and the relationship between emotion and cognition in the brain.

The simplest way to conceptualize the mapping between brain area and behavior is to assume a one-to-one mapping between an area and its function (e.g., amygdala <–> fear). It is readily apparent, however, that brain regions are involved in many functions, and that functions are carried out by many regions. More generally, therefore, the mapping between structure and function is both *pluripotent* (one-to-many) and *degenerate* (many-to-one). The combination of the two indicates that there are no "necessary and sufficient" brain regions. Based on these notions, I have argued elsewhere that a network perspective is needed for the understanding of the interactions between emotion, motivation, perception, and cognition (Pessoa 2008; 2009; 2010a; Pessoa & Engelmann 2010). Briefly, networks of brain regions collectively support behaviors (Fig. 1). Hence, the network itself is the unit, not the brain region. Processes *P* that support behavior are not implemented by an individual area, but rather by the interaction of multiple areas, which are dynamically recruited into multi-region assemblies.

I use the term "process" instead of "function" or "computation" because a process emerges from the interactions between regions, as in "emergent property" (Bressler & Menon 2010). Furthermore, a process is viewed as a useful external description of the functioning of the network, and not necessarily as a fixed internal computation implemented by the network (Thompson 2007; Thompson & Varela 2001). In this context, the suggestion by Lindquist et al. of *psychological primitives* is problematic, as the mind should not be viewed as constructed of atomic constituents in the manner that physicists conceive of matter, for instance.

Whereas a network perspective is needed for a fuller characterization of the mind-brain, it should not be viewed as a panacea. For one, the challenges posed by the many-to-many mapping between regions and functions is not dissolved by the network perspective. Indeed, one should not anticipate a one-to-one mapping when the network approach is adopted – counter to the recent trend of labeling networks with specific functions; see examples in Bressler and Menon (2010). Additionally, decomposition of brain regions in terms of meaningful clusters, such as the ones generated by community-finding algorithms (Newman 2010), does not by itself reveal "true" sub-networks. Given the heterarchical and multi-relational relationship among regions, multiple decompositions will offer different "slices" of the overall connectivity space. In what follows, I briefly discuss some repercussions of a network perspective to the understanding of the relationship between emotion and cognition.

First, given the extensive interactions among brain regions, the emphasis shifts from attempting to understand the brain one region at a time, to understanding how coalitions of regions support the mind-brain. Insofar as brain regions are not the unit of interest, they should not be viewed as "cognitive" or "emotional." Traditionally, however, regions whose function involves homeostatic processes and/or bodily representations have been frequently viewed as "emotional," whereas regions whose function is less aligned with such processes have been viewed as "cognitive."

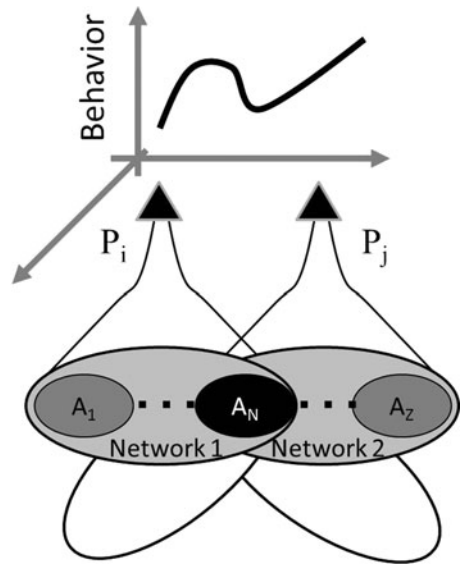

Figure 1 (Pessoa). Structure-function mapping. Networks are dynamically formed when areas (A_1, A_N, A_z) coalesce into temporally stable groupings. Area A_N (in black) is part of multiple networks. P_i, P_j = processes (see text).

Second, the architectural features of the brain are such that they provide *massive* opportunity for cognitive-emotional interactions (Modha & Singh 2010). These interactions are suggested to involve all brain territories. For example, extensive communication between the amygdala and visual cortex exists, and efferent amygdala projections reach nearly all levels of the visual cortex (Amaral et al. 2003). Thus, visual processing takes place within a context that is defined by signals occurring in the amygdala (as well as the orbitofrontal cortex, pulvinar, and other regions), including those linked to affective significance (Pessoa & Adolphs 2010). Therefore, vision is never pure vision, but is *affective vision* – even at the level of primary visual cortex (Damaraju et al. 2009; Padmala & Pessoa 2008). Cognitive-emotional interactions also abound in the prefrontal cortex, which is thought to be involved in abstract computations that are farthest from the sensory periphery. More generally, given inter-region interactivity, and the fact that networks intermingle signals of diverse origin, although a characterization of brain function in terms of networks is needed, the networks themselves are best conceptualized as neither "cognitive" nor "emotional."

Third, regions that are important for affective processing appear to be exceedingly well connected (e.g., Petrovich et al. 2001; Swanson 2000). This suggests that these regions have important "quasi-global" roles and that this is an important feature of this class of region. However, regions traditionally described as "emotional" are not the only ones that are highly connected. Highly connected regions are encountered throughout the brain, including in the occipital, temporal, parietal, and frontal lobes, in addition to the insula, cingulate, thalamus, and regions at the base of the brain (Modha & Singh 2010).

Fourth, emphasizing only interactions between brain regions that are supported by direct, robust structural connections is misleading. For one, the strength of functional connectivity is equally important, and at times will deviate from the strength of the structural connection (Honey et al. 2007). Architectural features guarantee the rapid integration of information even when robust structural connections are not present, and support functional interactions that are strongly context dependent. This is illustrated, for example, by the "one-step" property of amygdala–prefrontal connectivity – amygdala signals reach nearly all prefrontal regions within a single connectivity step (see Averbeck & Seo 2008).

Fifth, taken together, these considerations suggest that the mind-brain is *not* decomposable in terms of emotion and cognition. In other words, the neural basis of emotion and cognition should be viewed as governed less by properties that are intrinsic to specific sites and more by interactions among multiple brain regions. In this sense, emotion and cognition are *functionally integrated systems*, namely, they more or less continuously impact each other's operations (Bechtel & Richardson 2010). As suggested by Bechtel and Richardson, "The problem is then not one of isolating the localized mechanisms, but of exhibiting the organization and the constituent functions… [A]n explanation in terms of organization supplants direct localization" (p. 151).

The construction of emotional experience requires the integration of implicit and explicit emotional processes

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Abstract: Although we agree that a constructivist approach to emotional experience makes sense, we propose that implicit (visceromotor and somatomotor) emotional processes are dissociable from explicit (attention and reflection) emotional processes, and that the conscious experience of emotion requires an integration of the two. Assessments of implicit emotion and emotional awareness can be helpful in the neuroscientific investigation of emotion.

Lindquist et al. are to be commended for meticulously integrating comprehensive reviews of basic emotion theory with detailed meta-analyses from the neuroimaging of emotion literature. Using the extant neuroimaging literature, they cogently argue that neuroimaging evidence does not support the locationist view that specific brain circuits underlie specific emotional experiences or perceptions. Although this conclusion is not necessarily the final word on the question, as acknowledged by the authors, given the early state of brain imaging technology, the target article makes a convincing case that alternative formulations of the neural basis of emotion and emotional experience are needed.

In general we agree with Lindquist et al. that a constructivist approach to emotional experience makes sense. Indeed, in 1987 one of us described a constructivist model of emotional experience driven by language (Lane & Schwartz 1987). Where we disagree, however, is in the specific content of the constructivist model that is proposed. Throughout their article, Lindquist et al. assume that emotion must, at a minimum, be associated with the conscious experience or mental representation of emotion ("core affect") that is valenced and associated with some degree of arousal. The authors also hold that further differentiation of experience results from linguistically determined categories of specific emotion that do not have any real existence in nature. While we agree that the differentiated experience of emotion is largely language-driven, our primary concern is that the nature of the process of the construction of emotional experience is, in our view, more complex than Lindquist et al. assert.

With the discovery that the vast majority of cognition does not occur consciously, and that each of the steps in the generation and unfolding of an emotional response involves information processing of some kind, one of us has argued that the distinction between implicit and explicit processes, a cornerstone of modern cognitive neuroscience, also applies to emotion (Lane & Nadel 2000). According to this perspective, the visceromotor and somatomotor manifestations of emotion may occur in the absence of emotional experience, and constitute implicit emotional responses.

There is now a considerable literature supporting this view. In a comprehensive review on emotional experience, Lambie and Marcel (2002) concluded that a two-level model of emotional experience is needed that can account for unconscious emotion, that is, emotional responses without conscious experience or awareness (see also Kihlstrom et al. 2000; Lane 2008; LeDoux 1996). Over the past 25 years or so, academic research has been conducted on implicit affect, that is, spontaneous affective reactions associated with changes in peripheral physiology and/or behavior that are not associated with conscious emotional experiences (cf. Quirin et al. 2009a; Winkielman & Berridge 2004; Zajonc 2000). Lindquist et al. do not discuss the potential relevance of this distinction between implicit and explicit emotion processing for the analysis of neural correlates of emotion.

Furthermore, many decades of research preceding the modern era of neuroimaging demonstrated the evocation of visceral and somatomotor expressions of emotion in brainstem stimulation studies of laboratory animals (LeDoux 1996). Although these phenomena cannot be scientifically linked to reportable experiences, they nevertheless are the bodily expression of emotion. We believe that implicit emotion, consisting of the visceromotor and somatomotor expressions of emotion, which may or may not be valenced, constitute the foundation upon which more differentiated emotional experience is built. Moreover,

subcortical structures including the thalamus, hypothalamus, amygdala, and periaqueductal gray likely do contribute to the generation of undifferentiated emotional responses that are not associated with emotional experiences (Lane 2008). Many brainstem structures are not well-visualized using modern imaging techniques, which may help to explain the under-emphasis of these phenomena by Lindquist et al.

According to this alternative perspective, the conscious experience of emotion (which could include core affect) requires communication between subcortical and cortical structures, both paralimbic (anterior cingulate, insula, orbitofrontal cortex) and neocortical (medial prefrontal cortex). During attentional awareness, when individuals explicitly focus on their affective reactions, the dorsal anterior cingulate cortex is active (see Phan et al. [2004] for a meta-analysis), Furthermore, three different imaging studies have demonstrated that healthy individuals who are more emotionally aware engage the anterior cingulate cortex, particularly the dorsal portion, to a greater extent during emotional arousal (Frewen et al. 2008; Lane et al. 1998; McRae et al. 2008). In addition, reflective awareness of emotion involves the creation and integration of conceptual representations of emotional experiences that will affect the interpretation of future emotional experiences. Reflective awareness typically requires participation of structures in the paracingulate sulcus including the dorsomedial prefrontal cortex (Gusnard et al. 2001; Lane et al. 1997; Ochsner et al. 2004a). These two levels of explicit processing are superimposed upon and integrated with implicit affective processes. In this sense, conscious emotional experiencing is a constructive process that integrates implicit and explicit affect.

We propose that the investigation of how elementary affective processes develop to become full-blown emotional experiences may provide additional insight into the degree to which emotions are constructed psychologically. In this context, relating implicit measures of emotion such as the Implicit Positive and Negative Affect Test (Quirin et al. 2009a) to brain activity might be promising. Notably, the factor structure of this reliable indirect test divides into two types of implicit affect, positive and negative (see also Cacioppo et al. 1999; Gray & McNaughton 2000; Watson et al. 1999), suggesting that valence becomes part of emotional responses prior to the construction of emotional experience (see Quirin et al. [2009b] for relationships of implicit but not explicit affect with cortisol; also see Zajonc 2000). Furthermore, the neural correlates of emotional responses can be investigated as a function of individual differences in emotional awareness (Lane et al. 1990). Such approaches may contribute to the disentangling of the functional components of emotion, including somatic processes (peripheral physiological arousal and action tendencies), specific emotional experiences of a single type, blends of emotional experience, as well as regulation processes, all of which are typically implicated in affective responses and their neural correlates.

A systems approach to the brain basis of emotion also needs developmental and locationist views – the case of Tourette's Syndrome

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Abstract: The closeness of somatosensory phenomena and emotional states can be critically extended into a clinical perspective by referring to Tourette's Syndrome (TS). Two examples are discussed in this commentary: (1) the neurodevelopmental approach to the pre- and post-tic sensorimotor urges, and (2) the TS treatment with deep brain stimulation. It is shown that in TS, both views (locationist and constructionist) need to be combined along the lifespan in order to get a more realistic picture of the brain basis of emotion.

Lindquist et al. touch upon the closeness of and the interaction between somatosensory phenomena and emotional states (see target article, sect. 5.2). They refer to the anterior insula as a body-based, affectively guided attentional system, and thus present the insula as an integrational area for certain aspects of emotion, cognition, and movement, supporting their constructionist view. I would like to critically extend this aspect into a clinical perspective using data from research in Tourette's Syndrome (TS), a complex developmental neuropsychiatric disorder with motor and vocal tics as core symptoms (Cath et al. 2011; Müller-Vahl et al. 2011; Roessner et al. 2011a; 2011b; Verdellen et al. 2011).

Besides its overt tics, TS shows a covert drumbeat of sensorimotor phenomena such as unpleasant inner urges, with the consequence of acting out a tic in order to reach a "just right" somatosensory feeling for the patient's own bodily well-being. So far, it is assumed that the insula (in concert with the supplementary motor area and anterior cingulum) plays a central role in this respect (Münchau et al. 2011). This fits with the fact that electrical stimulation to the anterior insula may lead to visceral sensations such as feelings of movement, tension, twitching, and tingling (see sect. 5.2 of the target article), which may be reported by patients with TS as an announcement of a tic. It is likely that in TS the insula represents the pathophysiological link between the disturbance of the "sensorimotor-loop" related to the sensorimotor dissonance, which TS patients may realize around their tics, and the "affect-loop" related to cognitive-emotional dissonance in obsessive-compulsive behavior/disorder (Rothenberger et al. 2007), thus explaining why the "just-right" procedure in TS, although it mimics ritualized-compulsive behavior, prevails without any anxiety.

The general pre-tic body signal awareness in TS appears around the age of 10 years (i.e., several years after tic-onset), closely followed over time by the specific awareness of inner pre- and post-tic sensorimotor phenomena (including urges). There is no relationship between these phenomena and the duration of TS. Hence, usual cognitive brain development is the most important factor in order to explain this observation (Banaschewski et al. 2003). This highlights that one could optimize the constructionist hypothesis while using a neurodevelopmental approach. One should consider that local brain systems are sequentially more and more coordinated in order to finally form high-functioning, flexible constructionistic brain networks without losing locationist accounts. This view can be represented best by looking at the brain as an oscillatory system (Rothenberger 2009).

A further example of TS may show how locationist and constructionist approaches need each other. "In 1999 for the first time (thalamic) deep brain stimulation (DBS) was suggested as an alternative therapeutic option for treatment resistant, severely affected patients with TS" (Müller-Vahl et al. 2011). The different local targets used (e.g., globus pallidus internus, nucleus accumbens) lead to more or less similar clinical results. This is probably because all selected targets belong to the ventral striatal-thalamocortical circuitries, which are thought to be the basic dysfunctional system in TS. The DBS story elucidates that certain local "nodes" or "areas" may be essential for certain brain systems, suggesting a locationist view within a constructionist approach.

In sum, the case of TS, with its complex neurobiology and behavior, underlines that both views (locationist and constructionist) need to be combined along the lifespan in order to get a more realistic picture of the brain basis of emotions, cognitions, and movements. In this respect, I agree with the authors that, in addition to these considerations, the actual context is also very important, as even subliminal contextual features can unconsciously bias the biology of brain systems at work (Banaschewski et al. 2008).

The role of the amygdala in the appraising brain

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Abstract: Lindquist et al. convincingly argue that the brain implements psychological operations that are constitutive of emotion rather than modules subserving discrete emotions. However, the *nature* of such psychological operations is open to debate. I argue that considering appraisal theories may provide alternative interpretations of the neuroimaging data with respect to the psychological operations involved.

Affective neuroscience has considerably extended our knowledge of the emotional brain during the last two decades. Most of the work in this domain has consisted of searching for discrete dedicated brain systems underlying each basic emotion, using as evidence either neuropsychological dissociations (see Calder et al. 2001) or brain imaging results (see Vytal & Hamann 2010). Although this approach has extended our knowledge of the emotional brain, it has been strongly challenged by both empirical results and conceptual analyses (for details, see Sander, in press). Given that research on the brain basis of emotion has only rarely been explicitly considered in relation to psychological theories of emotion, the general aim of the current target article by Lindquist et al. is very beneficial to emotion research.

Lindquist et al. convincingly argue that we need to consider how the brain implements psychological operations that are constitutive of emotion rather than modules subserving discrete emotions. However, the nature of such psychological operations is open to debate. The authors only oppose their psychological constructionist view to the locationist view. Here, I argue that appraisal theories provide alternative interpretations to those offered by both the basic emotions perspective and by the authors. Lindquist et al. do not consider what can be seen as the third major research tradition in addition to "basic emotion" models and "core affect" models: namely, appraisal models. As a justification, the authors argue that: "Relatively little work from an appraisal perspective has investigated the brain basis of emotion (although see Sander et al. 2003; 2007). Therefore, we do not discuss appraisal models further in this article" (sect. 2, para. 2). I feel that, although an affective neuroscience approach to appraisal mechanisms is relatively recent (see Sander et al. 2005), many appraisal mechanisms (e.g., novelty detection, intrinsic pleasantness, or goal-relevance) have in fact been the focus of intense empirical research in cognitive and affective neuroscience, but typically without links being made directly to emotion elicitation (see Sander, in press). In addition, some studies have explicitly tested appraisal-driven hypotheses (e.g., Grandjean & Scherer 2008). As described below, conceptual analyses and empirical research have also pointed to a role of particular brain structures (e.g., the amygdala) in specific appraisal mechanisms (e.g., relevance detection).

Where Lindquist et al. do consider alternative interpretations of their results (sect. 6.1), they consider alternative methodological interpretations of the *absence* of findings supporting basic emotions theories, but they do not consider alternative conceptual interpretations of the *presence* of their meta-analytical findings. Consider the authors' conclusion concerning the brain region that has most clearly been associated with emotion in the literature: the amygdala. The authors write that their meta-analytical finding "is consistent with our hypothesis that the amygdala responds preferentially to salient exteroceptive (vs. interoceptive) sensations" (sect. 5.1, para. 6). Attributing a key role to the amygdala in processing saliency of exteroceptive stimuli indeed characterizes this brain structure with respect to a specific psychological operation, rather than to a basic emotion. Historically, the amygdala was typically associated with one emotion: fear. Associating a basic emotion to a specific brain system was consistent with basic emotion models (see Ekman 1999, p. 50). A common view has been that the amygdala is central to a "fear system," or even a "fear module" (Öhman & Mineka 2001). However, the lack of empirical evidence to conclude that the amygdala is specific to fear led scholars such as Kringelbach and Berridge (2009) to consider that equating the amygdala with fear is one of those "overly simple equations between neurobiology and psychology that merge into myth" (p. 481).

In the framework of appraisal theories of emotion, Sander and colleagues have argued that the computational profile of the amygdala is best characterized as default detection of stimuli appraised as relevant, given the individual's current concerns, such as goals, needs, and values (Sander et al. 2003; see also, Sander, in press). The idea that the amygdala is critical for relevance detection is grounded in appraisal models of emotion (see Frijda 1986, p. 390; Sander et al. 2005). Therefore, an alternative interpretation of the function of the amygdala that does not advocate a specific role of the amygdala for *fear* can be offered from an appraisal perspective. I believe that there is an interesting distinction between our analysis of the function of the amygdala and the authors' suggestion that the amygdala is associated with the psychological operation of "core affect" (see Figure 2 of the target article). Indeed, Lindquist et al. define "core affect" as the mental representation of bodily sensations that can be experienced as feelings of hedonic pleasure and displeasure with some degree of arousal. However, the very notion that a bodily sensation is mentally represented implies that a bodily response has been elicited *before* interoception could possibly lead to experienced feelings. In our account, relevance detection is supposed to be primary to the mental representation of bodily sensations because it is supposed to be involved in the *elicitation* of the emotional response, including the generation of bodily sensations. When considering conceptualization/categorization, Lindquist et al. "hypothesize that this psychological operation makes a prediction about what caused core affective changes within one's own body or what caused the affective cues (e.g., facial actions, body postures, or vocal acoustics) in another person" (sect. 3, para. 6). By contrast, appraisal theories are not typically concerned with how an individual *predicts* the cause of an affective change, but rather, with how a relevant event actually *causes* an affective change (see Moors 2009; Scherer & Ellsworth 2009). When the authors attribute a saliency processing function to the amygdala, it makes a critical theoretical difference whether they consider the role of saliency in (1) categorizing an external event as being a potential cause of an *already present* core affect, or rather in (2) the context-sensitive evaluation of an event as a function of the current concerns of the individual, which *causes* a change in the affective response, the latter being very much in line with appraisal theories of emotion.

Functional specialization does not require a one-to-one mapping between brain regions and emotions

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Abstract: Lindquist et al. have assumed that functional specialization requires a one-to-one mapping between brain regions and discrete emotions. This assumption is in tension with the fact that regions can

have multiple functions in the context of different, possibly distributed, networks. Once we open the door to other forms of functional specialization, neuroimaging data no longer favor constructionist models over natural kind models.

According to *natural kind models*, discrete emotions "exist in the brain or body and cause changes in sensory, perceptual, motor, and physiological outputs" (Barrett 2005, p. 257). According to *psychological constructionist models*, discrete emotions lack neural and bodily signatures, and "do not have ontological status as causal entities" (Barrett 2006a, p. 46). Lindquist et al.'s specific proposal is that emotions emerge when a more basic state of core affect – a blend of hedonic and arousal values – is conceptualized as an instance of a discrete emotion category such as fear or anger.

The two models make different predictions concerning the relation between brain and emotions. Natural kind models posit functionally specialized brain systems responsible for the production of the outputs of distinct discrete emotions. Constructionist models do not posit such functionally specialized brain systems, assuming that emotions emerge from brain systems dedicated to more basic psychological processes (e.g., core affect, categorization).

Lindquist et al. take neuroimaging data to favor constructionist models over natural kind models. This is because they consider the latter to be committed to what I call *radical locationism*, the hypothesis that discrete emotions consistently and specifically correspond to distinct brain regions. A brain region corresponds to an emotion *consistently* just in case it shows increased activation for every instance of that emotion, and *specifically* just in case it shows increased activation only for instances of that emotion. This amounts to positing a *one-to-one mapping* between single brain regions and discrete emotion categories.

Lindquist et al. have argued that there is no one-to-one mapping between single brain regions and discrete emotions such as fear, disgust, anger, and so on. For instance, the amydgala does not show increased activation in all and only cases of fear; the anterior insula does not show increased activation in all and only cases of disgust; the orbitofrontal cortex does not show increased activation in all and only cases of anger; the pregenual anterior cingulate cortex and subgenual anterior cingulate cortex do not show increased activation in all and only cases of sadness. At the same time, brain regions can be functionally *selective* for certain discrete emotions: they can occur *preferentially* – rather than *exclusively* – when a particular discrete emotion occurs.

I agree that *radical locationism* is false, and that regions consistently activated by discrete emotions are, at best, functionally selective for them. But I do not consider this to be a fatal strike against natural kind models, and a reason to become a constructivist. Natural kind models can endorse hypotheses about functional specialization other than radical locationism which are compatible with the neuroimaging data.

My central suggestion is that we should focus on networks rather than on single brain regions. This is because brain regions do not have functions in isolation, but rather in the context of the networks to which they belong (cf. Pessoa 2008). Furthermore, we should not expect functionally specialized networks to be neatly localizable anatomically. Functional specialization can be *multilocal* (Mundale 2002) rather than *radically localized*: the brain regions whose joint activation plays a given function can, in principle, be distributed across the brain.

Lindquist et al. are open to the possibility that there may be "widely distributed" networks for discrete emotions, but argue that their existence "would be consistent with a psychological constructionist . . . view" (sect. 6.1, para. 4). I strongly disagree. Constructivism posits that discrete emotions are not causal entities in their own right, but rather, effects of more basic psychological processes. The existence of networks for discrete emotions would strike at the heart of this idea, vindicating instead the natural kind proposal that discrete emotions have ontological status as causal entities and are driven by distinctive, though distributed, neural mechanisms.

Once we shift to a networks approach, a one-to-one mapping between single brain regions and discrete emotions is no longer the litmus test for functional specialization. Understood broadly, functional specialization has to do with the existence of physically discrete regions in the brain – possibly distributed – that play at a time a function that is not played by other physically discrete regions. The point is that a functionally specialized brain region X can play more than one function, depending on which other regions it is co-activated with, without this calling into question that X fulfills a specific function in the context of a given network at a given time.

Even brain regions commonly considered to be paradigms of functional specialization can fulfill multiple functions depending on the networks with which they are affiliated. For example, Broca's area has long been considered functionally specialized for language, but it is also involved in other functions, such as movement preparation and action sequencing (cf. Anderson 2007). As Lindquist et al. point out, even the primary visual cortex contains "neurons that participate in different neural assemblies associated with different functions" (sect. 6.1, para. 1). Yet, we still consider it functionally specialized for vision.

This leads me to question the principle that "[s]upport for a psychological constructionist view. . .would be found if the same brain region(s) were involved in realizing instances of several emotion categories – and, furthermore, if the brain region(s) are more generally important to realizing a basic psychological operation" (sect. 4, para. 1). If a brain region can have a function in a network at a particular time without being exclusively dedicated to that function at all times, it is hard to see why some region X could not be *functionally specialized* for, say, disgust – good candidates for this role would be regions consistently and selectively activated by disgust – despite the fact that X is not *functionally specific* to disgust. The fact that a brain region may be involved in networks associated with other discrete emotions and with more basic psychological processes is compatible with the fact that *at a specific time* it is functionally specialized in producing disgust (or another discrete emotion).

These remarks seem to suggest that proponents of natural kind models should hypothesize a *one-to-many* mapping between single brain regions and fear, anger, disgust, and other emotions. Things are, in my view, more complicated, because our current ontology of discrete emotions is most likely inappropriate for the study of functional specialization. I have argued elsewhere that *folk emotion categories* are too heterogeneous for scientific purposes, and should be split into more homogenous subcategories that capture theoretically distinct types of emotion, types of fear, types of anger, and so forth (Scarantino, in press).

This is to say that the mapping between single brain regions and fear, anger, disgust, and so on, may ultimately turn out to be *many-to-many*. Not only could the (possibly distributed) networks functionally specialized for a given discrete emotion include brain regions that play other functions in other emotional and non-emotional networks (the one-to-many aspect), but there could also be multiple brain networks functionally specialized for anger, for fear, for disgust, and so on (the many-to-one aspect). This would call into question the opportunity of using folk emotion categories for the study of discrete emotions.

Whether these speculations will prove to be correct remains to be empirically determined. What we can say at this stage is that neuroimaging data have yet to tip the balance for either constructivist or natural kind models, and that both approaches continue to be worth pursuing in our efforts to understand the brain basis of emotions.

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Neuroscience findings are consistent with appraisal theories of emotion; but does the brain "respect" constructionism?

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Abstract: I reject Lindquist et al.'s implicit claim that all emotion theories other than constructionist ones subscribe to a "brain locationist" approach. The neural mechanisms underlying relevance detection, reward, attention, conceptualization, or language use are consistent with many theories of emotion, in particular componential appraisal theories. I also question the authors' claim that the meta-analysis they report provides support for the *specific* assumptions of constructionist theories.

Lindquist et al. mostly use their impressive meta-analysis to contrast their constructionist approach with all other emotion theories, which are credited with a "locationist" account ("discrete emotion categories [. . .] are consistently and specifically localized to architecturally defined brain locales or anatomical networks"; see "Definitions" box in section 3). This is a gross misrepresentation of the architectures of classic emotion theories, many of which suggest that emotion episodes are driven by complex interactions of multiple mental and somatic systems (cognitive, motivational, autonomic, motor) that are *not* specialized for emotion. This precludes the assumption of emotion-specific brain centers. In consequence, the authors' fundamental premise is untenable, the results of their meta-analysis being consistent with many different emotion theories (Moors 2009).

This is particularly true for componential appraisal theories (see Ellsworth & Scherer 2003; Roseman 2011; Roseman & Smith 2001), which Lindquist et al. credit with a locationist account (see sect. 2, para. 1). For example, the component process model (CPM) of emotion (Scherer 1984; 1986; 2001; 2009b) postulates that the dynamic unfolding of emotion episodes is driven by parallel appraisal processes at different levels of brain organization that sequentially evaluate objects and events for their novelty, intrinsic pleasantness, and goal conduciveness; and for compatibility with self-concept, social norms or values, and the individual's coping potential. These appraisals are *content criteria*, not specialized mechanisms for emotion, based on the general information-processing machinery of the brain (perception, association, schema matching, prediction error checking, categorization, inference). For example, contrary to Lindquist et al.'s claim (sect. 3, para. 5), novelty checking is not a new, unique, emotion-specific mental operation – there are many studies on novelty processing in cognitive (see Ranganath & Rainer 2003) and affective neuroscience (Balderston et al. 2011).

The appraisal results cumulatively produce changes in several subsystems of the organism, including the motivational system (action tendencies, e.g., approach/avoidance), support system (endocrine, autonomic, and somatic nervous systems), and monitoring system (subjective feeling). These bodily response patterns are fed back recursively into the appraisal process through interoception. This appraisal-driven *synchronization* of subsystems that are not specialized for emotion, but have specific functions for the organism's different needs, *constitutes* the emotion episode. The monitoring system integrates proprioceptive information about changes in different systems, producing unique mental representations (qualia). If the subsystem synchronization level is sufficiently high, the emotion process may enter consciousness and engender categorization (which can be nonlinguistic) and – if the context requires communication of the emotion to others – labeling with emotion words or metaphors (Grandjean et al. 2008; Scherer 2009b). This architecture is "constructionist" in the dictionary sense of the word.

Contrary to Lindquist et al.'s claim (sect. 2, para. 2) that an appraisal approach hypothesizes that "dedicated cognitive mechanisms automatically make meaning of a stimulus and trigger the corresponding discrete emotion," the CPM includes all levels of processing (from sensory motor to propositional) and does not assume dedicated mechanisms or a limited number of automatically triggered discrete emotions. On the contrary, the CPM allows for an almost infinite number of different emotion episodes, given the recursive, emergent character of the sequential-cumulative configuration of appraisal results and consequent patterning of response systems (Scherer 1984). This architecture also accounts for the prevalence of blended or mixed emotions (e.g., see Scherer & Ceschi 2000; Siemer et al. 2007).

Also contrary to the authors' claim (sect. 2, para. 2), several attempts have been made to muster neuroscience support for appraisal predictions (Sander et al. 2005; Scherer 1993; Scherer & Peper 2001). Furthermore, many CPM hypotheses have been experimentally tested using neuroscience methods. For example, Grandjean and Scherer (2008), using EEG, chronometrically confirmed the predicted sequence of novelty, intrinsic pleasantness, and goal-conduciveness checks. Dan Glauser and Scherer (2008) showed that the conscious experience of feeling an emotion is associated with specific brain wave oscillations (see Scherer [2009b] for a recent overview of empirical evidence for CPM predictions).

The authors' meta-analysis lends further support to the CPM (whose architecture makes it incompatible with locationist assumptions). For example, low-level relevance detection in the amygdala, interoceptive representation in the insula, integration of subsystems in the orbitofrontal cortex (OFC) or networks relative to attention or conceptualization, are entirely consistent with the model's architecture. As most emotion theories assume, implicitly or explicitly, that in many contexts, emotional experiences are categorized, conceptualized, and labeled (see Scherer 2009b, pp. 1318–24), any evidence for brain mechanisms subserving these operations is equally consistent with those theories. Demonstration of the neural underpinnings of categorization or conceptualization does not privilege any theory on why or when categorizations and conceptualizations lead to specific effects.

One wonders whether the meta-analysis supports *specific* claims of the authors' theory, which assumes that a "conceptual act" is needed to *constitute* the emotion. This "definitional act" is immune to empirical evidence of any kind. Contrary to established usage, it limits the term to conceptualized subjective experience or feeling, thereby excluding objectively measurable emotion episodes in nonhuman animals, nonverbal children, and normal individuals who cannot or do not conceptualize such episodes as emotion feelings.

Furthermore, the meta-analysis does not reveal stringent evidence for "core affect," presumed to be a fundamental feeling architecture organized as an orthogonal valence × arousal system. As valence is generally considered a fundamental organizing criterion for affectivity, any evidence for brain mechanisms underlying valence processing is consistent with virtually all theories of emotion. It does not lend further credence to the monolithic "core affect" notion.

The authors admit that core affect might need to be broken down into more basic mechanisms, such as approach- versus avoidance-related states (sect. 6, para. 5). Such action tendencies (Frijda 2007) are postulated by most emotion theories, and the underlying brain mechanisms are among the first to have been examined (Davidson 1993). The authors also state that the amygdala "realizes" core affect (mostly when "the rest of the brain cannot easily predict what sensations mean," sect. 5.1, para. 2) by detecting relevance (which they call "salience," covering only one aspect of relevance). This position, together with emphasis on the brain's "making meaning" of exteroceptive and interoceptive information, comes close to a rudimentary

componential appraisal theory, although vague references to context-bound categorization and conceptualization do not facilitate development of testable nomothetic predictions.

Invariants of human emotion

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Abstract: Because of the complexity of human emotional responses, invariants must be sought not in the responses themselves, but in their generating mechanisms. Lindquist et al. show that functional locationism is a theoretical dead end; their proposed mechanistic framework is a first step toward better models of emotional behavior. We caution, however, that emotions may still be quasi-natural *perceptual* types.

Herb Simon (1990) proposed more than twenty years ago that the problem of identifying invariants of human behavior is complicated by the fact that people are adaptive systems with highly flexible behavior. Invariants must therefore be sought not in the behaviors themselves, but in the mechanisms that guide the processes of individual adaptation: the mechanisms of intelligence. This stance supported the search for mechanistic models of cognition, in the form of computational models (Baars & Franklin 2009; French 1995; Holland et al. 1986; Newell 1990; Rumelhart et al. 1986; Simon 1979).

Researchers have become increasingly aware that emotions cannot be considered separable from cognition (Damasio 2000; Dolan 2002; LeDoux 1996; Phelps 2006). Emotional states are the lens through which perceptions become thoughts, and thoughts become actions. A more thorough understanding of human behavior requires the incorporation of emotion into our mechanistic models. We adapt Simon's proposition thus: The problem with identifying invariant emotional categories is complicated by the fact that people are adaptive systems, whose emotions are highly flexible. Invariants must therefore be sought in the mechanisms that allow them to produce these feelings – the mechanisms of affective responses.

Lindquist et al. show that locationism, and a strict adherence to a natural kinds view of emotions, is likely a theoretical dead end. More importantly, they seek to replace a modular view of emotion states with a mechanistic model of how those states come to be generated. The model they have proposed is vague, perhaps necessarily so, as emotional categories are emergent phenomena of a highly complex system. There may be flaws in their model, and it may eventually be discarded in favor of a better model. It is clear, however, that the incorporation of emotions into a mechanistic understanding of cognition requires a generative model of emotional states. The invariants of emotions are to be found not in the discrete emotional categories, but in mechanisms that generate emotional responses.

A functionalist perspective of emotions as natural kinds assumes, at minimum, that each emotion (or "family of emotions"; Ekman 1992) is controlled by an independent cognitive system, even if those systems are not locationally isolated. This is an organizational blueprint which is attractive in its clarity and simplicity, but which strikes us as unlikely. The brain's cognitive architecture is a system of vast complexity shaped by millions of years of evolution. It is unlikely that the emergence of each emotion involved a separate evolutionary trajectory, each with its own selection pressures and phylogenetic path. Instead, we consider far more plausible the evolution of a generative, multipurpose emotion system. This is supported by the principle that it is much easier to evolve a self-organizing complex system that can adapt to varied environments than to specify a unique module for every contingency (Kauffman 1995; Schank 2002).

Although emotions may not represent natural kinds in terms of brain organization, we caution against the complete dismissal of the idea of basic affective categories; emotions may exist as quasi-natural *perceptual* kinds without necessitating functional locationism. There is cross-cultural recognition of the meaning of emotional expressions (Ekman 1989), even if these expressions must be exaggerated to be identified (Barrett 2006a). This may reflect more about the *perception* of emotions than about their expression. Humans are natural pattern classifiers, and the ability to readily detect broad emotion categories from facial expressions makes sense from an adaptationist perspective (Daly & Wilson 1995).

Social animals are well served by the quick assessment of meaning behind others' emotional expressions, even if fast mapping means a loss of nuanced information. The sight of a confederate running towards you with a look of panicked horror yields an altogether different reaction on your part than a look of joyful excitement. We think it unlikely that emotional categories are largely driven by language, as proposed by Lindquist et al., as well as by Barrett and colleagues previously (Barrett et al. 2007b). Rapid identification of emotional cues is clearly adaptive, possibly even more for individuals without language, and moreover is present in nonhuman primates (Tate et al. 2006). If recurring families of cues become strongly associated with certain types of responses, evolution may select for enhanced recognition of those cues on the part of the observer, and, if successful transmission is adaptive, more precise production on the part of the transmitter (Bateson 2004; Maynard Smith & Harper 2003). Therefore, *rapid* identification of important emotional cues may embody quasi-natural kinds as emergent properties of fast-acting response systems, and it seems to us that this hypothesis has not been damaged by Lindquist et al.'s analysis.

Finally, we hope that this target article represents the first step toward rigorously tested generative models of emotion. Although we can say little about this here, understanding the nature of emotions is critically important for producing explicit models of human and animal social behavior, which is in turn crucial for gaining insight into and predictions about our world.

A rapprochement between emotion and cognition: Amygdala, emotion, and self-relevance in episodic-autobiographical memory

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Abstract: Lindquist et al. remark that not all fear instances lead to heightened amygdalar activity and, instead, point to roles of the amygdala in detecting "motivationally salient "or "emotionally impactful" stimuli. By reviewing research on the amygdala's functions in episodic-autobiographical memory, we further emphasize the involvement of the amygdala in coding the subjective relevance and extracting the biological and social significance of the stimuli.

As Lindquist et al. describe, oscillations between localization and anti-localization of functions characterize brain research. Localizationists argue that circumscribed brain lesions can abolish a function throughout a life-span. Frequently cited is the patient H.M. who, after undergoing bilateral resection of the medial temporal lobes, developed life-long anterograde amnesia (Markowitsch & Staniloiu, in press). Functional neuroimaging data also point to specialized regions being selectively activated during face processing (Kanwisher 2010). At the other pole of the dialectics, Chow (1967) argued that if a lesion in a brain region has no particular effect on a function, it cannot be concluded that this region is irrelevant for that function in non-damaged individuals. Second, if a lesion does influence the performance of a task, this does not mean that that region is the only structure involved in the task. And last, and perhaps most important, brain tissue damage cannot clarify the function of a brain area, because it destroys what it aims to study – that brain area. Functional imaging studies, showing that widespread regions in the brain are activated even when performed tasks are simple, and electrophysiological experiments (Bartlett & John 1973; John 1972) support views of the brain acting in a Gestalt-like fashion.

Generally, no brain region can act alone *in vivo*, and, especially for more complex functions, a multitude of brain regions act in concert or within a neural network (Cramon & Markowitsch 1992; Fink et al. 1996; Markowitsch 1994; Schulte-Rüther et al. 2010; Staniloiu & Markowitsch 2010). This was already suggested by Papez in 1937 in his seminal paper entitled "A proposed mechanism of emotion" (Papez [1937], overlooked by the Lindquist et al. in the target article). Processing of episodic-autobiographical memories requires attention and concentration, self-reflection and emotional colorization (Markowitsch & Staniloiu, in press) (see our Fig. 1).

Emotional evaluation and tagging are important for both formation and retrieval of episodic-autobiographical memories, and they engage limbic system regions (Markowitsch 1999). Within these regions, the amygdala constitutes a cornerstone as it represents the major hub for channeling sensory information of biological or social personal significance to storage in networks located primarily in neocortical areas. Behavioral studies performed in patients with Urbach-Wiethe disease, a rare genetic condition leading to bilateral calcification of the amygdala (Cahill et al. 1995; Markowitsch et al. 1994) emphasize the role of the amygdala for evaluating the salience of newly incoming information and extracting those portions which appear worth being remembered.

Several combined neuroimaging and behavioral studies of healthy subjects or patients showed amygdalar engagement in episodic-autobiographical mnemonic processing. Brain mapping of the time course of episodic-autobiographical memory retrieval revealed modulation of amygdala activity by judgments of emotional intensity of autobiographical memory. This occurred early in the process of retrieval, before (healthy) participants in the study signaled the full assemblage of autobiographical memories (Daselaar et al. 2008). This finding is congruent with the proposed role of the amygdala in charging sensory information with appropriate emotional cues, in order to guide successful searching for and retrieval of emotionally significant events (Markowitsch & Staniloiu 2011).

Not all functional neuroimaging investigations of episodic-autobiographical memory retrieval evidenced amygdalar activation, due to differences in memory-testing methodology, imaging techniques' limitations, lack of control for retrieval perspective, or habituation of amygdala responses to emotional material over time (Markowitsch & Staniloiu 2011). An increase in right amygdalar activity was found in subjects who retrieved episodic-autobiographical memories from a first person perspective, in comparison to those who retrieved them from a third person perspective (Eich et al. 2009), suggesting a higher degree of subjectively perceived emotionality associated with the first type of memories. Neuroimaging studies showed activation of the amygdala as a function of personal relevance or self-involvement of the recalled material. One study comparing the retrieval of autobiographical episodes with the retrieval of fictitious "episodes" revealed activation of the amygdala only during the recall of personal – that is, authentic – events, whereas the recall of fictitious material activated the retrosplenial/precuneus area only (Markowitsch et al. 2000). Personal relevance enhanced amygdala activity during the recall of the frightening event of September 11, 2001 (Sharot et al. 2007).

These results suggest that the amygdala has functions in coding the subjective relevance and social and biological salience of the stimuli, which might be reflected in its structure and hodology. The amygdaloid nuclei are heavily connected with subcortical and cortical areas, including regions involved in self-referential

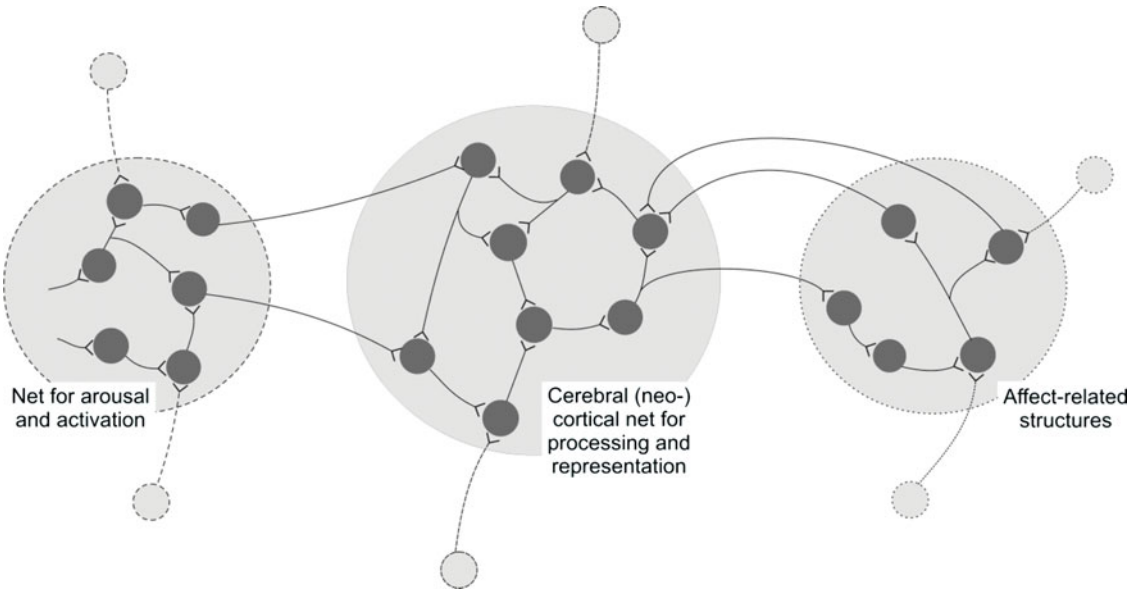

Figure 1 (Staniloiu and Markowitsch). A schematic sketch of a neural net composed of three interacting subsets.

processing, such as the ventro-medial prefrontal cortex. From the neocortex, fibers arising from the multisensory posterior association cortex, but in part also from primary sensory regions (olfaction), project to the amygdala. Subsequently, the amygdala receives largely preprocessed sensory input, which then provides a basis for the amgdala to extract the personal biological and social significance of the environment. Nevertheless, the amygdala is not the only structure which plays a role in this process of evaluation. A working tandem may, for example, exist between the amygdala and septal nuclei. A damaged amygdala dampens emotional evaluation (Siebert et al. 2003) whereas damaged septal nuclei enhance it (Cramon & Markowitsch 2000). A patient with septal damage, for example, could not tolerate listening to an emotional story with negatively valenced content, because of overwhelming perceived emotionality (Cramon et al. 1993).

In conclusion, our findings from patients with Urbach-Wiethe disease and from studying episodic-autobiographical memory with various functional imaging techniques in different populations, support Lindquist et al.'s view that the amygdala is not simply an emotional brain structure, but integrates emotion with cognition. This view was, in our case, significantly shaped by work with patients with relatively selective amygdala lesions. This work enabled verifying hypotheses, which may not have been possible by simply resorting to data from imaging studies. Despite using various mathematical models to interpret functional magnetic resonance imaging data, it is still difficult to infer causality from function–structure correlations obtained with brain imaging; therefore, additional experimental techniques (e.g., transcranial magnetic stimulation) may need to be used to confirm whether a brain region is necessary or specific for a given function.

Feeling the strain: Predicting the third dimension of core affect

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Abstract: This commentary (1) raises the question about the possible conflation of core affect with the neural representation of interoceptive changes in regard to whether biological value is subpersonal or must be experienced, and (2) proposes that Wundt's third dimension of core affect – strain-relaxation – can be accounted for in the target model under a generalised predictive model of attention.

I am very much in sympathy with the model of emotion presented by Lindquist et al. in the target article, which successfully manages to integrate psychological data on emotion with current neuroscientific findings, and provides the possibility of grounding phenomenological accounts of intentionality and mood in the biology of affect. My points in this commentary are therefore not intended as criticisms of the model. I offer instead a clarificatory question, and a proposal for developing the model further.

I start by flagging a concern about the possible conflation of core affect with the representations of afferent homeostatic information. Core affect is an explicitly psychological phenomenon, yet the target text is sometimes ambiguous as to whether it denotes: (1) a psychological feeling state, (2) the representation of interoceptive information, or (3) the actual bodily state. For example, take this statement from the discussion of situated conceptualisation in section 3:

> In emotion, we hypothesize that this psychological operation makes a prediction about what caused core affective changes within one's own body or what caused the affective cues [. . .] in another person. (sect. 3, para. 6).

Here, "one's own body" must either mean the physiological body or the brain. The first option appears to conflate core affect (the feeling of physiological changes) with affect (the physiological changes themselves). The second option implies the quoted statement should read, "a prediction about what caused core affective changes which arise as a result of changes in one's body being represented in the brain." But if so, then it is unclear whether the prediction underpinning the situated conceptualisation is supposed to concern bodily changes, the representation of those changes, or the feeling of those changes. Some clarification here would be helpful.

Although I agree that core affect is *grounded* in interoception, conflating the two risks obscuring the mechanisms for representing biological value; is it (1) core affect – the feeling of the interoceptive information – that is linked to sensory information, or (2) the neural representation of interoceptive information? It might be suggested that the feeling of the interoceptive changes just *is* the representation of those changes, but it seems unlikely that this is what the authors are claiming, since this would mean that their use of "feeling" did not necessarily imply that this information was experienced. While this is not an unprecedented use of the term (see Damasio 1999), the authors state specifically in the target article that core affect is a psychological phenomenon which always presents itself in experience, either in the foreground or the background. This raises an important question: Is the biological value that is being imposed on the environment as a result of situated conceptualisation an experienced value or can it be restricted to some sub-personal domain?

The second question that I want to raise concerns the dimensions of core affect. Barrett has argued elsewhere (Barrett & Bliss-Moreau 2009) that Wundt's original dimensions of affect should be translated as valence, arousal, and intensity. But Barrett and Bliss-Moreau reject intensity as a dimension, arguing that it is realised by the ends of the dimensions of valence and arousal. While Wundt does speak of intensity and quality in regard to affective and sensational systems, he does not do so in such a way as to suggest that these are the dimensions of affect (see Wundt 1897, sect. 3). Wundt's dimensions of feelings are: (1) pleasurable and unpleasurable; (2) arousing and subduing; and (3) strain and relaxation (Wundt 1897, sect. 7.7). Although (1) and (2) neatly map on to valence and arousal respectively, as Barrett and Bliss-Moreau suggest, I do not think that (3) maps on to intensity. I suggest rather that, where arousal is a distinct affective dimension likely to be grounded in the afferent wing of the continuous – but varying – activity of the sympathetic nervous system, and valence may be grounded in the motor aspect of the homeostatic/interoceptive loop (accounting for its relation to approach/withdrawal states), Wundt's third dimension of affect can be grounded in the force with which prediction error is being reduced.

According to the generalised predictive coding framework for neuroscience (Bar 2009a; Friston 2009; Friston & Kiebel 2009), unexpected sensations are intrinsically motivating in virtue of the nervous system's function being to reduce error in predictions. According to such a story, any sensation that was not predicted will inherently motivate the system either to move and act, or to update its hypothesis concerning the cause of the predicted sensations. Action and/or hypothesis change are mandated until there is no error and the sensation corresponds to that which was predicted. Feldman and Friston (2010) argue that attention may be the process of optimising the post-synaptic

responsiveness of the units reporting prediction errors. What this means in practice is that if the system regards some sensory information as high-grade (hence reliable), it can increase the gain on the error-units reporting prediction error, thus giving added weight to that sensory data. In such a case, the units encoding that error become highly responsive (synaptic gain). This means they exert a greater force by which to resolve prediction errors. The searchlight of attention thus gets progressively finer until all prediction errors have been resolved, or a greater error arises elsewhere.

I propose that the directions of strain and relaxation correspond to the force and resolution of synaptic gain as evidenced in attention and the corresponding affective experience of being drawn towards that which captures our attention, or releases us. This fits Lindquist et al.'s compelling model of many-layered predictions generating situated conceptualisations. It also neatly incorporates attentional phenomena into the more basic operations of prediction and corresponding experience within the domain of core affect.

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What's in a baby-cry? Locationist and constructionist frameworks in parental brain responses

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Abstract: Parental brain responses to baby stimuli constitute a unique model to study brain-basis frameworks of emotion. Results for baby-cry and picture stimuli may fit with both locationist and psychological constructionist hypotheses. Furthermore, the utility of either model may depend on postpartum timing and relationship. Endocrine effects may also be critical for accurate models to assess mental health risk and treatment.

To differ with Lindquist et al., perhaps both locationist and constructionist frameworks for the brain basis of parental emotion have utility, depending on stimulus parameters, timing, and relationship. For example, consider the baby-cry, a single primal signal that for an infant, not capable of complex interactive social signaling, must serve to attract the attention of new parents at the risk of adverse parental responses or drawing predators (Soltis 2004; Swain et al. 2004). Thus far, there is evidence that the parental brain basis of baby-cry-elicited emotions may fit with locationism; involving a simple set of circuits, including the amygdala and insula. Several groups have been studying the brain basis of maternal response to baby-cry and related behaviors within a relatively locationist framework (Swain et al. 2007). Initially, the thalamocingulate circuit for emotion response and regulation in mammals was supported (Lorberbaum et al. 2002; MacLean 1990), but several other brain regions, including parts of the amygdala, insula, and striatum/nucleus accumbens (NA) have also been shown to respond to baby-cry (Swain et al. 2011). Responses in the medial frontal cortex and striatum also predict parental mood and anxiety (Swain et al. 2008).

However, as the infant develops nuanced social signals in the context of a growing attachment, psychological constructionist frameworks to understand parental brain responses to baby stimuli, in accordance with Lindquist et al., may be more appropriate, in which emotions can be elicited that are intimately tied to prior experiences and conceptualization. For example, early life events may influence current brain activity in cortical regions, that have not been the subject of rodent literature. Some such connections have recently been discussed with respect to maternal sensitivity. (For thorough reviews, see Barrett & Fleming 2011; Swain 2011). In support of such early-life effects on complex brain functions, a recent study has shown that maternal brain structure and functional responses to the mother's own baby's crying in the early postpartum period varied according to mothers' perceived maternal care quality in their own childhood in accord with a constructionist framework (Kim et al. 2010b). In this study, mothers who reported having received greater maternal care in childhood showed higher gray matter density, in a range of higher cortical and executive function areas, including the insula, superior and middle frontal gyri, orbital gyrus, superior temporal gyrus, and fusiform gyrus.

Strikingly, some of these morphological and functional changes in the maternal brain are also associated with the concurrent conceptualization of positive maternal thoughts toward their babies (Kim et al. 2010a). In this first prospective longitudinal study, gray matter volume increased over the first few months postpartum (from 2–4 weeks to 3–4 months) in the insula, prefrontal cortex, parietal lobes, and midbrain areas. Further work is required to elaborate the constructionist framework of relation between concurrent positive thoughts about one's baby and increased gray matter volume in multiple core affect regions of the hypothalamus, substantia nigra, and amygdala, or to support locationist approaches for certain experimental paradigms (Kim et al. 2010a).

In evaluating locationist versus constructionist frameworks of the brain basis of emotion, a meta-analysis of brain imaging studies may be informed by the critical contributions of certain hormones just beginning to be included in such studies. For example, we contend that multiple hormonal systems related to parental motivation, including oxytocin, must be considered in frameworks of the brain basis of emotion. The neurohormone oxytocin, for example, is one of the major factors that accounts for variations in regulating parental emotions during parent–infant interactions (Feldman et al. 2010). Another aspect of a new mother's emotion regulation is her recent mode of delivery, such that vaginal versus cesarean deliveries are associated with higher oxytocin (Marchini et al. 1988). Consistent with this, mothers who have had vaginal deliveries show greater brain responses to baby-cries in the insula, striatum, and anterior cingulate cortex (Swain et al. 2008) than do mothers who have had cesarean deliveries. Furthermore, regardless of delivery type, mothers known to show higher oxytocin during breastfeeding (Nissen et al. 1996), also have higher brain responses to their own baby's crying than do formula-feeding mothers, in the insula, striatum, amygdala, and superior frontal gyrus (Kim et al. 2011). Although requiring replication, these experiments support a constructionist framework that includes hormone levels – in addition to maternal brain responses in the cingulate, striatum, and hypothalamus when shown baby pictures, some of which responses vary with individual differences in oxytocin and concurrent attachment (Strathearn et al. 2009).

Indeed, the key dimension of hormone responses in developing a comprehensive framework for understanding the brain basis of emotions is underlined by a causal relationship between oxytocin and women's brain responses, in two recent studies. First, in a randomized control trial (Riem et al. 2011), experimentally elevated oxytocin versus placebo resulted in increased responses to the cries of unrelated babies, in the inferior frontal gyrus and insula, and decreased responses in the right amygdala. This study shows that oxytocin may modulate maternal behaviors, that is, enhance positive motivation by sensitizing care-related insula activity and reduce negative motivation

by desensitizing anxiety-related amygdala responses. Second, in a study by Naber et al. (2010), administration of oxytocin increased sensitive parental emotions and behaviors, assessed by videotaped play session. In fact, infant pictures by themselves have been shown to exert similar modulation of maternal brains (Bartels & Zeki 2004; Strathearn et al. 2008).

The use of baby-cry to stimulate emotions in parents may present some challenges to the psychological constructionist framework, and require locationism for certain paradigms. Perhaps then also, locationism may still be useful in understanding the effects of interventions – such as for complex multi-system and time-delayed effects. Indeed, some recent studies interpret brain imaging data on basic face responses (Canli et al. 2005) or intervention effects in emotion response circuits according to a locationist model, whether using structural or functional approaches (Chua et al. 2011; Peterson & Weissman 2011). Ultimately, more research, probably including endocrine parameters, is needed to clarify the utility of locationist versus constructionist frameworks according to different paradigms.

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Narrative constructions and the life history issue in brain–emotions relations

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Abstract: Emotional reactions are rather flexible, due to the schema-like organization of complex socio-emotional situations. Some data on emotion development, and on certain pathological conditions such as alexithymia, give further support for the psychological constructivist view put forward by Lindquist et al. Narrative organization is a key component of this schematic organization. The self-related nature of narrative organization provides scaffolding to the contextual dependency of emotions.

Lindquist et al. very clearly argue for a psychologically constructed vision of emotion by their re-analysis of the enormous and still growing neuroimaging literature on emotions, and by challenging the locationist views. Our aim is to recall that arguments for contextual flexibility and social determination are to be found as well in the literature on emotion development and cultural determination.

Emotions in norm transmission. In the transmission of cultural norms regarding emotion behavior, emotions are set in a reinforcement scene in socialization. Caregivers may react to the emotion expressions of infants and children with reward, punishment, overriding, neglect, or magnification (O'Neal & Magai 2005). Positive parental response to emotion provides models for adaptive emotion regulation strategies (Gottman et al. 1997), helping children to refine and rehearse emotion management skills. However, undesired emotion expression may be met with rejection, or criticism, from parents who do not foster the ability to identify and communicate emotions, or who may encourage the suppression of emotion, or the use of avoidant or aggressive emotion regulation strategies (Eisenberg et al. 1996; Gergely & Watson 1999; Kench & Irwin 2000). As a consequence, undesired positive or negative emotions may not be differentiated properly, remaining undifferentiated, or become associated with another emotion. Primary emotion-related self–other representations resulting from this process (Gergely & Unoka 2008) are embedded in wider contextual narrative structures. These in turn create autobiographical self-representations (Berán & Unoka 2005), correlated with the activation of distributed networks in the brain (Conway 2005).

Narratives and emotions. Several studies, such as the one by Oppenheim et al. (1997), have shown that narrative organization, as revealed in the joint story-telling of 4–5-years-old children and their parents, correlates with emotional integrity. However, the formation of contextual narrative structures of emotions may result in pathological outcomes when affected by strict cultural norms regarding emotion display (e.g., Allan & Gilbert 2002; Chaplin et al. 2005; Le et al. 2002), specific caregiver–child temperament constellations (e.g., Coplan et al. 2009), and caregiver pathologies of emotion regulation (e.g., Gergely & Unoka 2008; Silk et al. 2011). In the latter case, the caregiver, due to his/her own mental disorder (e.g., depression, psychosis, personality disorders) is unable to help the child learn to regulate his/her own emotional responses.

Culture plays a central role in shaping how emotions are experienced and expressed. Certain cultures or subcultures restrict the open experience and expression of emotions, which may result in the pathology of alexithymia: a difficulty in identifying one's feelings and distinguishing them from bodily sensations, as well as a difficulty in communicating one's emotions to others (Le et al. 2002). Alexithymia was found to be associated with difficulties in detection of the facial expression of anger, sadness, and fear (Prkachin et al. 2009). Alexithymia was also negatively correlated with activation to sad and happy faces in several brain regions (Reker et al. 2010), which are described by Lindquist et al. as the brain regions forming part of the distributed network realizing core affect. Hence, as a consequence of this type of socialization, negative emotions may remain undifferentiated, and this is correlated with a less-differentiated brain activation pattern, which would show up in fMRI studies.

Anger expression determined by social ranking is another point in the differentiation of emotions in social contexts. Occurrence of complex negative affect patterns is evident in sensitivity to social put-downs (Gilbert & Miles 2000): feeling anxious or distressed about being put down is highly correlated with feeling angry/irritated. Allan and Gilbert (2002) found that self-perceptions of inferior rank and feeling trapped affects anger suppression. The *rank of the target* also affects anger expression: People who respond angrily to social put-downs tend to suppress their anger more when they are frustrated by a higher-rank target, compared to a lower-rank one. This result is in accord with animal studies of aggression which show marked variations in aggression expressed up and down the ranks (Archer 1988).

In response to the stimulus of an angry facial expression in an fMRI study, the brain reactions of persons within a rigid rank-relational schema will be different for a person of lower-rank compared to one of higher-rank. People with a submissive self-schema in their narrative self-representation would react with fear, whereas those with a dominant self-schema would react with anger. Thus, in addition to emotion activation, a facial-expression stimulus activates a social relational self–other schema – an interactional pattern, which activates different neural networks of the brain. The representation of rank order and the appropriate reaction to the facial expression of the angry other is embedded in narrative self-representations, which are further complicated by cultural norms concerning appropriate emotion expression.

Parental reactions to child emotions also play an important socializing role in the development of children's emotional self-regulation (Eisenberg et al. 1996). Mothers with a history of childhood depression are less likely than mothers without such history to respond in supportive ways to children's negative emotions, and are more likely to magnify, punish, or neglect negative emotions (Silk et al. 2011). These parental responses one year later were associated with children's internalizing symptoms, which suggest that in the development of internalizing pathologies, atypical socialization of emotion may play a role. Thus, if the caregiver rejects the child's display of a negative emotion, such as anger, then it may become associated with other emotions, such as fear, separation anxiety, or guilt, due to their contextual embeddedness in narrative structures. The anger schema of such individuals includes fear, and related self-to-other and other-to-self affective representations (Gergely & Unoka 2008).

Internalization disorders, avoidant attachment style, and adult avoidant and dependent personality disorders are examples of such an association of emotions. These emotion scripts raise the methodological problem that the emotion activated in the experimental setting will consist of the quick activation of two emotions – anger and fear, for instance, since they share a common neural network. Consequently, because of the low temporal resolution of fMRI, the neural correlates of the two emotions can hardly be differentiated.

All of these factors suggest that the psychological constructivism suggested by Lindquist et al. can be given a more detailed socio-cultural interpretation in this respect. The relativistic and contextual interpretation provided for the brain basis for emotions could converge with developmental and clinical contextual interpretations.

Neuronal deactivation is equally important for understanding emotional processing

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Abstract: In their analyses of the neural correlates of discrete emotionality, Lindquist et al. do not consider the numerous drawbacks to inferring psychological processes based on currently available cognitive neurometric technology. The authors also disproportionately emphasize the relevance of neuronal activation over *de*activation, which, in our opinion, limits the scope and utility of their conclusions.

Although we commend Lindquist et al. for addressing several ambitious areas of inquiry, including neural activation of discrete emotions, we have several reservations with the authors' empirical assumptions, and with their subsequent conclusions, which leave us with more questions than answers. One concern is that the authors' treatment did not incorporate the numerous drawbacks to inferring psychological processes based on currently available cognitive neurometric technology. Conventional brain imaging devices, for instance, have relatively poor temporal resolution as compared to actual electrical transfer and inter-neuronal communication. The inability to precisely monitor the temporal sequence of localized brain activity combined with the spatial limitations of these techniques severely limits the ability to measure how environmental energy (e.g., task-induced stimuli) is transformed into psychological energy. Moreover, individuals show great variability in anatomical positioning (Amunts et al. 2004), and it remains unclear just how and to what extent the types of data that are relied upon to infer brain activation (e.g., relative oxygen blood flow) are representative of, and can be used to map the structure, stages, and feedback of, neural networks.

Another important limitation of the authors' current analyses (and of the broader cognitive neuroscience literature as a whole) is the disproportionate emphasis on measuring brain activation versus brain *de*activation. These efforts are based, in part, on the perspective that psychological functioning (both excitatory and inhibitory firing) requires activation processes, and that the absence of neural activity implies the nonexistence of psychological functioning. However, it is well established that certain behaviors, such as lying still with one's eyes closed or passively viewing a visual stimulus – standard baseline control conditions in neuroimaging experiments – are associated with decreased regional brain activity (Raichle et al. 2001). Investigations of the visual and auditory cortices have likewise shown reciprocal deactivation when the other region is activated (Laurienti et al. 2002; Lewis et al. 2000). Tomasi and colleagues (2006) interpret cross-modal inhibition as intentional deactivation of contra-brain regions, so as to decrease interference from non-relevant neural processes (Tomasi et al. 2006). Lindquist et al. do not consider the concept of intentional deactivation in their analyses, nor do they consider how regions, such as the anterior cingulate cortex (ACC), which make tradeoffs between facilitating either cognitive or emotional processing (only one function is possible at any given time) may have affected their results (Drevets & Raichle 1998). Task difficulty, possibly related to differential remote memory retrieval, influences ACC activity (Paus et al. 1998), and tasks that require greater cognitive demands may confound analyses intended to measure emotional processing.

In other words, brain *de*activation may provide just as important information as activation patterns provide for understanding emotion-processing mechanisms (see also Davidson 1998; Davidson & Irwin 1999). Consider the case of amygdala activation, which is a well-established concomitant of threat processing and subsequent elicitation of *fear* and *disgust* responses, as the authors show. What the authors fail to address, however, is the importance of amygdala deactivation, which the authors also show is indicative of experiencing *anger* and *joy*. This makes sense, as both anger and joy are demonstrative of empowerment, and therefore systematically occur in response to the appraisal of non-threatening stimuli (Vigil 2009). Lesion and neuroimaging studies show that amygdala activation is necessary for detecting distrust, and when the amygdala is deactivated or impaired, individuals are more likely to infer trustworthiness and benign attributes in others (e.g., Adolphs et al. 1998; Engell et al. 2007; Winston et al. 2002; Zald 2003). It is therefore likely that the inhibition or absence of amygdala activity may facilitate specialized and functional elements of social cognition, particularly in social situations that favor cooperative over avoidant behavioral strategies.

Unfortunately, we are uninspired by the utility of the authors' currently described "conceptual act model" of discrete emotionality, which can arguably be interpreted as another form of "locationist" model, substituting broader psychological constructs (e.g., memories, knowledge) for the more specific constructs (e.g., natural kinds) that the authors argue against. Moreover, the authors' core hypothesis that "people make meaning" out of physiological states, subsequently resulting in emotional experiences, is indistinguishable from an embodied-simulation model of emotional processing (e.g., see Niedenthal et al. 2010), which we have argued against elsewhere (Vigil & Coulombe 2010). In particular, we showed that the mere evaluations of core trait impressions of *trustworthiness* and *capacity* are both necessary and sufficient for predicting interpersonal dispositions (e.g., to affiliate or avoid; see e.g., Cacioppo et al. 1999; Gray 1994; Lang et al. 1990) and discrete emotional reactions (e.g., felt disgust vs. sympathy) towards others (see also, e.g., Fiske

et al. 2006; Rosenberg et al. 1968; Todorov 2008; Vigil 2009; Wojciszke 2005). Therefore, the recourse to prior experience and personal meaning of a given context may not always be necessary for explaining how and why emotional and broader affective-behavioral processing occurs.

Lindquist et al. have built their argument such that if criteria for the locationist argument are not met, it is assumed to be support for the psychological constructionist perspective. This is misleading, and fails to recognize other possible explanations. One alternative explanation, of many, is H. C. Barrett's (2005) analogy that cognitive modules use a template matching system similar to that used by enzymes. In modular models of human cognition it is not *necessary* that brain activity be localized to specific areas across participants due to factors such as plasticity and the brain's reorganizational capabilities in response to injury (e.g., H. C. Barrett 2005; H. C. Barrett & Kurzban 2006; Marshall 1984; Robertson & Murre 1999). Modularity is a central concept of the computational model of the mind, and although there is disagreement as to the extent to which the mind is modular, there is broad agreement that it is at least somewhat modularized (e.g., Barrett & Kurzban 2006; Hagen 2005). Future research that can incorporate multi-dimensional techniques, such as activation-based techniques (e.g., neuroimaging) and disruption-based techniques (e.g., temporary lesion methods), will eventually elucidate the form and function of discrete emotionality, as well as guide the development of clinical applications for cognitive neuroscentific research (e.g., Pouratian et al. 2003; Rorden & Karnath 2004).

Timing: A missing key ingredient in typical fMRI studies of emotion

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Abstract: Lindquist et al. provide a compelling summary of the brain bases of the onset of emotion. Their conclusions, however, are constrained by typical fMRI techniques that do not assess a key ingredient in emotional experience – timing. We discuss the importance of timing in theories of emotion as well as the implications of neural temporal dynamics for psychological constructionism.

Lindquist et al. have advanced a very thoughtful review on the brain bases of emotion garnered from neuroimaging. Their summary should prove useful for investigators interested in understanding the functions of the brain regions involved with emotions. We also believe that the current state of neuroimaging evidence provides fairly compelling support for their psychological constructionist theory of emotions. We argue, however, that the current state of neuroimaging evidence, while necessary, is not sufficient to fully support their theory. Neuroimaging has thus far only provided a snapshot of the initial onset of emotion, while ignoring one of the most fundamental elements of emotional experience – time.

Emotions happen over time: from the initial appraisal of an emotional event that can occur within hundreds of milliseconds (Schupp et al. 2000) to event-induced moods that can endure for weeks (McCullough et al. 2007). Although often ignored empirically, time is an important parameter in most major theories of emotion. Process-models of emotion have emphasized that emotions endure and change over time, and that temporal approaches to understanding emotions should yield discoveries about how emotions are fundamentally processed (Larsen et al. 2009). For example, it has been shown that longer enduring emotional experiences can be predicted by the importance and initial intensity of the emotion-eliciting situation (Verduyn et al. 2009). Beyond emotional reactivity, timing has also proved critical for understanding emotional regulation (Gross 2001). Whether people enjoy the social, psychological, and physiological benefits of cognitive reappraisal (vs. suppression) depends, in part, on when they attempt to regulate their emotion (Gross 2001). Finally, and particularly relevant to the present target article, it has been suggested that the timing of emotion is a key mechanism underlying the neural bases of individual differences in emotional experience (Davidson 1998).

Despite the obvious importance of timing in understanding emotional experience, it has been mostly ignored in neuroimaging studies. The reason is simple: Traditional functional magnetic resonance imaging (fMRI) statistical techniques do not estimate time. The overwhelming majority of fMRI analyses model the data with canonical gamma-based hemodynamic response functions (HRFs) (Friston et al. 1994). When these canonical HRFs are used to model the data, only one parameter – height – is allowed to vary. The temporal parameters of the HRF, such as the delay and dispersion, are typically fixed, which does not allow for the estimation of possible temporal dynamics of the underlying blood oxygenation-level dependent (BOLD) response. There is a delay from neural activity to measurable BOLD response (Bandettini et al. 1993), so these time-invariant HRFs only assess hypothetical neural activity occurring in the first second after stimulus onset while failing to account for significantly delayed neural responses or neural responses of longer duration. This means that fMRI studies of emotion in large part fail to capture the development of emotional experience beyond the initial response to the emotional stimulus.

Recent studies that have used time-varying HRFs show why estimating temporal features of the BOLD response may prove critical to test Lindquist et al.'s conclusions. In one study, we used the summation of three inverse-logit curves as a time-varying HRF (Lindquist & Wager 2007) to examine how the duration of BOLD activity relates to self-reported intensity of emotional experience (Waugh et al. 2010). First, we found that the insula exhibited extended duration of BOLD activity to more intense negative images. Lindquist et al. have proposed that the insula, as part of the *core affect* network, represents visceral arousal. This suggests that although visceral arousal can occur quickly, it can also be sustained for a significant period of time and, perhaps, lead to sustained insula activation. Second, we found that regions along the cortical midline, the medial prefrontal cortex (mPFC) and posterior cingulate cortex (PCC), also exhibited extended duration of BOLD activity to intense negative images. In conjunction with Lindquist et al.'s proposal that these regions are associated with the *situated conceptualization* of emotional experiences, this finding suggests that in intense emotional situations these structures may stay active to continually monitor the meaning of the situation to the self. Indeed, in another study examining neural responses during long periods (~2 minutes) of social evaluative threat, the mPFC was found to stay active for the entire duration of the stress period (Wager et al. 2009b).

These findings – that the insula and cortical midline exhibit extended duration of activation during intense emotion – offer an example of how estimating timing of emotion could support or challenge Lindquist et al.'s psychological constructionist argument. One supporting argument would be that each of these regions may be responsible for certain psychological constructs that, although enduring over time, do not fundamentally change. Thus, a snapshot of an emotion at any time point after the initial onset could still be a construction of these separable constructs. A potential challenge to this argument would be that these systems do behave very differently over time. Although the "making meaning" function of the cortical midline regions may persist over time, the very meaning that this system

generates may qualitatively change. Through these shifts in meaning, the cortical midline could alter the network of active regions by selectively enhancing or reducing the input from regions according to the relevance of their associated psychological constructs to the meaning being made about the situation. For example, the network of constructs associated with the initial response to a potential anger-eliciting situation (e.g., salience, attention, motivation) may, over time, become shaped to correspond to the increasing "anger-ness" of the situation (e.g., motivation, agency).

The above formulations are quite speculative; indeed, it is even unclear whether, if correct, they would support Lindquist et al.'s constructionist argument. Our purpose in presenting them is merely to emphasize the importance of assessing temporal characteristics of neural responses to emotion. Emotions develop over time, and understanding precisely how they do so will greatly improve our understanding of how they are constructed in the brain.

Need for more evolutionary and developmental perspective on basic emotional mechanisms

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Abstract: Lindquist et al.'s meta-analysis focuses on adult humans; the authors' emotion model might be strengthened by considering research on infants and animals, highlighting the importance of the limbic system. Reliance on the James–Lange theory is questionable; emotions typically occur instantaneously, with dubious dependence on bodily feedback for affect. Stronger evidence for localization might be obtained using more precise emotion terms and alterative localization methods.

We think Lindquist et al.'s model would benefit from a more evolutionary and developmental perspective (cf. Tinbergen 1951). Attention to emotion in infants and other species would highlight the continuity in emotional mechanisms from ancestral species and infants to adult humans. Then, more weight might be given to limbic system mechanisms and less to cortical processes. Certainly, people use the cortex to identify emotionally relevant stimuli on the basis of conceptual learning and cognitive interpretation, but the limbic system reacts emotionally to unconditioned stimuli such as tastes and facial expressions, to conditioned stimuli, and to stimulus familiarity (Campos & Barrett 1984; Zajonc 1994).

The authors assert that "emotion words are essential to our model" (sect. 3, para. 7) and claim that infants possess enough language capacity to experience emotion, but many emotions emerge by 9 months of age. Infant emotions, such as fear, unfold through epigenetic programs according to a precise, universal timetable (LaFreniere 2000; 2010; Sroufe 1996) well before the onset of language. Young infants rely mainly on subcortical behavioral mechanisms, not language (*infans*, L., without speech), for registering and communicating their specific emotional needs.

Likewise, vertebrates depend heavily on unlearned, limbic system responses to execute specific emotional behaviors such as fighting a rival (Butler & Hodos 2005; Tinbergen 1951). Identifying particular adaptive needs is not completely surrendered to the vagaries of cognitive interpretation and experience. Reptiles, lacking a neocortex and abstract cognitive abilities, nevertheless possess emotional systems for flight, attack, and feeding. Specific emotional behaviors and brain structures show considerable continuity across mammals (Panksepp 1998). Mammals possess reward and punishment limbic areas (Olds & Milner 1954) homologous to structures that, when stimulated in conscious patients, elicit reports of specific affects (anger: King 1961; fear: Gloor 1997; humor appreciation: Black 1982; Martin 1950). Specific affects also arise during psychomotor seizures (Gloor 1997).

The fact that the brain often instantly registers specific affects weakens the claim that interpretation is necessary for affective experience. The authors refer to interpretation of sensory feedback from the body and endorse the James–Lange position that affects occur *after* the motivated behavior and accompanying visceral changes. Presumably, discrete affects evolved to direct adaptive motivated behavior, so there would be little benefit from telling the brain what it should do after it has acted. In James' example, why would fleeing a bear be necessary for fear – if one froze in terror, would one not be afraid? People may reflect on their fear after escaping, but typically report having been terrorized immediately.

Cannon (1927) and Bard (1928) challenged James–Lange with laboratory research showing that affect precedes visceral adjustments. Visceral feedback takes several seconds – but affects are instantaneous, so visceral feedback cannot be the primary source of affect. In spinally transected experimental animals and patients, behavioral responses and affective self-reports are appropriate for the situation. Engaging in exercise with its visceral changes does not elicit particular affects. Of course, bodily input initiates some affects, such as low blood glucose or stomach contractions eliciting hunger. But hunger is not triggered *following interpretation* of feeding or visceral adjustments to food intake.

Recent evidence supporting Cannon and Bard comes from LeDoux (1996). A mammal receives emotionally salient information through sensory systems that activate the thalamus. There, a quick appraisal of the information takes place. If the stimulus constitutes a conditioned or unconditioned stimulus of, say, fear, a rat exhibits the panoply of fearful behaviors. The central nucleus of the amygdala orchestrates the various facets of the emotional response. The central gray activates the overt behavior of freezing, and the hypothalamus initiates visceral adjustments such as increased heart rate. But fear comes first: the affectively sensitive amygdala presumably registers fear before these behavioral and visceral events occur. LeDoux's model does not include feedback from the voluntary muscles or viscera to the limbic system. With the neocortex removed, a rat will still respond to appropriate fear releasers or conditioned stimuli. With the neocortex intact, it makes finer discriminations of these stimuli; it may not exhibit fear of a tone different from that which it was conditioned to fear. The neocortex also allows finer motoric responses. So the neocortex only refines emotional behavior, but is not the essential mechanism, which is limbic.

But why is so much of the brain, including the neocortex, activated by an emotional stimulus? Observable behavior consists of addressing specific emotional needs seriatim. Like other animals, we feed, sleep, mate, defend ourselves, compete, and so forth through the day. We use our neocortex to perform these behaviors more efficiently, but our behavior is motivated by the limbic system. Because it is for the fulfillment of biological needs that, arguably, our brains evolved, large areas of the brain, including language areas, are mobilized by emotional stimuli, especially verbal ones. We selectively attend to, recall, and react to emotionally salient stimuli. These reactions include not only affect but also visceral, hormonal, expressional, cognitive, mnemonic, and overt behavioral responses. This widespread activation of the brain makes it difficult to pinpoint affective experience, especially given the technical difficulties of neuroimaging subcortical structures. Affects may be better

localized by brain stimulation, experimental lesions, and clinical research.

Another problem is that the brain structures studied are highly differentiated. The amygdala has 15 nuclei (Gloor 1997) and is implicated in aggression and sexual behavior, not just fear. The orbitofrontal cortex is involved in pride and shame (Fuster 1997), as well as anger. Finer anatomical analysis might reveal more emotional specificity.

Also problematical are the emotion terms in Lindquist et al.'s meta-analysis. Whereas the amygdala is activated in fear, fear of giving a speech deactivates the amygdala. This is understandable if one thinks of the amygdala as mediating fear of bodily harm, not fear of *any* unpleasant outcome, such as embarrassment in this case (which might activate the orbitofrontal cortex). Many researchers relied on Ekman and Friesen's (1971) list of six emotions with universal facial expressions. Other emotions have no distinct facial expression, as Ekman (1994a) acknowledged, and some facial expressions – happiness and sadness – can be observed following *any* pleasant or unpleasant experience. More specific localization might result from using more precise emotion terms.

Authors' Response

What are emotions and how are they created in the brain?

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Abstract: In our response, we clarify important theoretical differences between basic emotion and psychological construction approaches. We evaluate the empirical status of the basic emotion approach, addressing whether it requires brain localization, whether localization can be observed with better analytic tools, and whether evidence for basic emotions exists in other types of measures. We then revisit the issue of whether the key hypotheses of psychological construction are supported by our meta-analytic findings. We close by elaborating on commentator suggestions for future research.

Philosophers, psychologists, and neuroscientists have debated the nature of emotion for centuries because it touches on our most precious questions. Do emotions show us to be the same or different from the rest of the animal kingdom? Do we respond automatically and reflexively to the world or do we have free will? Is it possible to have an objective science of subjective phenomena? How do we map psychological descriptions to physical measurements? These basic issues are at the foundation of the commentaries on our target article. We are grateful for the thought-provoking commentaries that provide us with the opportunity to clarify misconceptions, rectify ambiguities, address points of contention, and discuss exciting suggestions for applications and future directions of our model.

R1. Basic emotions versus psychological construction: Theoretical clarification

For several centuries, mental philosophers debated whether the human mind is populated by mental organs, each producing a specific kind of mental content ("faculty psychology"; e.g., Broca 1861/2003; Gall & Spurzheim 1809), or whether it is organized as a set of more basic, domain-general elements that together make a variety of mental states (e.g., Hartley 1749; Herbart 1809; Thorndike 1923; for reviews, see Klein 1970; Uttal 2001). As psychology moved from philosophy to empirical science, this debate was absorbed into its guiding theoretical assumptions, particularly in writings on the nature of emotion. Some writers argued that certain emotion categories have the status of mental faculties: independent and autonomous, hard-wired and innate, and psychologically elemental (e.g., Allport 1924; Lange 1885/1912; McDougall 1908). In modern times, this approach has become known as the *basic emotion* approach (e.g., Ekman 1972; 1992; Ekman & Cordaro 2011; Izard 1977; 1990; 2011; Lewis 2005; Panksepp 1998; 2007; Panksepp & Watt 2011; Tracy et al. 2010) or the *natural kind* approach (cf. Barrett 2006a). Others argued that emotions were produced out of a more basic set of psychological elements (e.g., Duffy 1934; James 1890; Wundt 1897/1998). Recently, this approach has become known as the *psychological construction* approach to emotion (e.g., Barrett 2006b; Russell 2003; for a discussion, see Gendron & Barrett 2009).

Just as there is variety in any category, both basic emotion and psychological construction models come in a variety of flavors (Table R1). These nuances can make the emotion literature difficult to understand for those who are not steeped in its history and debates. Most relevant to the discussion at hand, there is disagreement within the basic emotion approach about what makes certain emotions (but not others) basic (also see Ortony & Turner 1990). Some hold a strong localization hypothesis, such that all the emotional episodes belonging to a single emotion category (e.g., *fear*) are caused by neural responses in an anatomically defined location (e.g., Calder 2003; Davis 1992; Ekman 1999; Öhman & Mineka 2001). Other models hypothesize that each basic emotion should be localized to the firing of a (typically) subcortical circuit (e.g., Izard 2011; Panksepp 1998). Still others believe that emotions need not be localized in the brain to be natural kinds (e.g., Ekman & Cordaro, 2011; Lewis 2005). These latter models hold other hypotheses about what makes emotions biologically basic with naturally defined boundaries (e.g., synchronized patterns of autonomic response, specific facial expressions, etc.), and

Table R1. *Assumptions and testable hypotheses in Basic Emotion and Psychological Construction Models*

Features		Basic Emotion		Psychological Construction	
		Position	Commentators	Position	Commentators
1. Timing	A	Emotions are bounded mental events that unfold linearly over time.	Sander Scherer Waugh & Schirillo Vigil et al.	Emotions are not events with a clear start, middle and end. Core affect is constantly changing in a steady stream, as is conceptualization, and the two (along with other ingredients) influence one another according to a constraint-satisfaction logic.	
2. Uniqueness	H	Each emotion category refers to a unique mental state. These states are mental faculties – they are different in kind from one another, and from cognitions and perceptions.	Gardiner Sander Scherer Vigil et al.	Emotion, cognition, and perception are mental categories that are not respected by the brain; they are ontologically subjective categories that a Western mind uses to classify its own mental states. Minds in other cultures parse their mental states in using other categories.	Perlovsky Pessoa Smaldino & Schank
3. Modularity	H	Emotions are triggered in an obligatory way once a stimulus or its interpretation occur.	Caruana & Gallesse Gardiner Jablonka & Ginsburg Sander Scherer Swain & Ho Vigil et al. Waugh & Schirillo Weisfeld & LaFreniere	Emotions are constructed. This construction can be initiated by a shift in core affect or priming some conceptualization. Sometimes changes in core affect are conceptualized as emotion and at other times they are conceptualized as some other kind of mental state. A mind can have the capacity to emote without emotions being distinct kinds of mechanisms.	Cramer et al. Deshpande et al. Humeny et al.
4. Behavior	A	Emotions are behavioral adaptations to specific environmental challenges.	Caruana & Gallesse Jablonka & Ginsburg Weiseld & LaFreniere	Emotions are defined as behaviors when the goal is to highlight how human and nonhuman animals are similar. animals experience affect. This is a definitional move that cannot be empirically tested (we can test whether behavioral adaptations exist across species, but not that they are the proper definition of emotion). Ontologically reducing emotions to behavioral adaptations limits the scientific understanding of emotion in humans.	
5. Diagnostic Suites	H	Emotions have unique and specific manifestations, such as sets of facial actions that signal the internal state of the emoter, physiological patterns, or neurochemical signatures. These synchronized, coordinated "suites" of	Buck Button et al. Caruana & Gallesse de Gelder & Vandenbucke Jablonka & Ginsburg	Emotion categories (e.g., anger, sadness, fear) do not occur with consistent, specific patterns of facial actions, peripheral physiology, or neurochemicals. Facial actions can be used to symbolize an emotion.	Humeny et al.

(*continued*)

Table R1 (*Continued*)

Features		Basic Emotion		Psychological Construction	
		Position	Commentators	Position	Commentators
		response can be used to diagnose the presence of an emotion.	Quirin & Lane Scherer Smaldino & Schank Weisfeld & LaFreniere		
6. Variability	H	Variation of responses within a single emotion category is due to measurement error or regulation after the fact.	de Gelder & Vandenbucke Murphy et al. Scarantino Vigil et al. Weisfeld & LaFreniere	Variability within a single emotion category is the rule, not the exception. In emotion (e.g., anger), people feel and do many things. Responses are tuned to the situational context (and physiology follows behavior).	Button et al. Humeny et al. Smaldino & Schank Unoka et al.
7. Consciousness	H	Emotions arise from automatic mechanisms and can be unconscious, although the experience of emotion can occur in humans.	Kirov et al. Swain & Ho	Conceptual knowledge shapes core affect automatically, although it can be applied through conscious deliberate means. The resulting mental state is always consciously experienced. Sometimes emotion is experienced as a property of the world (e.g., a person is offensive, a situation is threatening, etc. At other times, an emotion can be explicitly labeled with an emotion word and experienced as one's reaction to the world.	Quirin & Lane
8. Localization	H	Emotions are consistently associated with specific islands of brain activation. . . .	Caruana & Gallesse Kirov et al. Weisfeld & LaFreniere	Emotions do not correspond in consistent and specific ways to increased activity within specific brain locations.	Cramer et al. de Gelder & Vandenbucke Deshpande et al. Humeny et al. Stanilou & Markowitsch Sander Smaldino & Schank Vigil et al.
	H	. . .or activation in specific, inheritable brain circuits or networks	Hamann Murphy et al. Rothenberger Scarantino Swain & Ho	An emotion, like all mental states, occurs as a brain state that is a dynamic convergence of interacting networks.	Deshpande et al. Hechtman et al. Pessoa
9. Evolution	A	Emotions are inherited adaptations that human and nonhuman animals share.	de Gelder & Vandenbucke	The architecture of the human mind is surely sculpted by important evolutionary factors, but it is highly unlikely that each emotion emerged as its own mechanism, with its own	Perlovsky

				selection pressures, along its own evolutionary path.	
		Jablonka & Ginsburg Smaldino & Schank Weisfeld & LaFreniere			
10. Generation vs. Regulation	H	Emotion generation processes are distinct from those used in emotion regulation. Regulation is sensitive to context, but generation is not.	Kirov et al. Quirin & Lane Smaldino & Schank Waugh & Schirillo Weisfeld & LaFreniere Buck	Emotion generation and regulation are realized by the same set of processes. As situated conceptualizations, both emotional experiences and emotion perceptions are sensitive to context.	Cramer et al.

Note. A = assumption. H = hypothesis.

we discuss the empirical status of these other hypotheses later in section R2. For the rest of the present section, we use Table R1 to launch a discussion of the commentaries that deal with basic emotion ideas or to contrast them to psychological construction. During this discussion, we emphasize how the two approaches compare in their assumptions and definitions (ideas that are not empirically verifiable; e.g., "emotions are behaviors") as well as their hypotheses (ideas that can be tested with data; e.g., "emotions are coordinated sets of physiology, action, and feeling").

R1.1. False dichotomies

By claiming that emotions are evolutionary adaptations (**de Gelder & Vandenbulcke**; **Jablonka & Ginsburg**; **Smaldino & Schank**; **Weisfeld & LaFreniere**), researchers often falsely assume that the basic emotion approach is the evolutionary approach and that psychological construction does not consider evolution as important. In reality, both approaches assume that the human mind was sculpted by evolutionary forces, but at issue is what, exactly, evolved (e.g., emotions or the more basic psychological ingredients that create emotions?).

Similarly, it is tempting to assume that the basic emotion approach is a natural science approach, whereas the psychological construction approach engages in extreme relativism (**de Gelder & Vandenbulcke**). Our model tries to traverse the biology–psychology divide by taking the position that (1) psychological elements can be mapped to activity in the nervous system (but probably not at the gross anatomical level or in a 1:1 manner); (2) the biological function of an individual brain region can always be described by its anatomical connections, but its psychological function should *also* include its functional connections (or neural context; McIntosh 2000); and (3) emotion categories, as complex psychological categories, are not psychological functions – they are collections of psychological events that are best explained as combinations of more basic psychological building blocks. These building blocks might be localized at the level of an anatomical or functional network. The psychological ingredients we have proposed in the target article and response to commentaries (core affect, conceptualization, language, executive attention, and sensory perception) are a first approximation, and we expect that these ingredients will be refined with future research.

A related idea is that the basic emotion approach is scientifically advantageous because it is easier to empirically disconfirm (e.g., a locationist hypothesis) when compared to the more flexible psychological construction approach (**Hamann**). The psychological construction framework is flexible by design, however, to explicitly account for the observed variability in emotional responding (Barrett 2009a). Given that we outlined our model in print only five years ago, and that psychological construction, as a definable scientific approach to emotion, has only been articulated within the last decade (e.g., Barrett 2006a; Russell 2003),[1] it is not surprising that more evidence is needed before we can be confident of its validity (see sect. R3.1). Furthermore, psychological construction

is more challenging to test precisely because we must measure variability (rather than looking for a small set of stable outcomes) and we must show that this variability is scientifically meaningful and not due to error. That said, it is not the case that any set of hypotheses will do. The a priori hypothesis at issue in our target article was that the same brain regions would be consistently active during a range of emotional experiences and perceptions, as we found in our meta-analysis. In other papers, we hypothesize that these regions become functionally coupled into multiple, large-scale networks and that these interconnected networks are the relevant functional units that constitute the human mind (see Barrett 2009a). We have further proposed that these networks dynamically configure during an instance of emotion (e.g., an instance of *anger*), but that the precise configuration would be tied to a specific situational context, rather than a broad psychological category (e.g., *anger*) (Wilson-Mendenhall et al. 2011).

It is also easy to assume that basic emotion approaches find scientific value in categories like *anger, disgust, fear*, and so forth, but that psychological construction models do not (**de Gelder & Vandenbulcke**; **Smaldino & Schank**). Indeed, it is often assumed that psychological construction models merely reduce discrete emotions to simple affective dimensions of valence and arousal (de Gelder & Vandenbulcke; **Buck**; **Scherer**). But psychological construction is an explicit attempt to integrate dimensional and categorical approaches to emotion. All psychological construction models assume that, at their core, emotional experience and perceptions contain a representation of the somatovisceral state of the body[2] (a point that both **Stapleton** and **Sander** question).[3] Bodily representations are then made meaningful as instances of discrete emotion (or as *cognitions*, *perceptions*, or even *physical symptoms*) (cf. Barrett 2009b). We hypothesize that these mental categories themselves are not given by nature, but live in the mind of the perceiver: we predict that there is no reliable, objective distinction between *emotions*, *cognitions*, *perceptions*, or *physical symptoms* as types of mental categories, although the individual instances within a category will vary (Barrett 2009b; Barrett & Bar 2009; Duncan & Barrett 2007; Pessoa 2008; also see **Pessoa**'s commentary). The instances of these categories are therefore important phenomena to be explained, but *emotions*, *cognitions*, *perceptions*, or *physical symptoms* are not causes or processes.

Because a key feature of psychological construction is the hypothesis that changing body representations are transformed into a discrete emotion via some kind of meaning-making process,[4] there is a temptation to assume that this meaning-making is deliberate, effortful, and the act of conscious labeling (**Quirin & Lane**; **Scherer**; **Smaldino & Schank**; **Weisfeld & LaFreniere**), whereas the basic emotion hypothesis is that emotions are automatically generated. Yet our psychological construction approach hypothesizes that conceptual knowledge shapes sensations from the body automatically, effortlessly, and continuously, just as top-down conceptual knowledge turns wavelengths of light into images and objects, and air vibrations into voices, music, and noises. Of course, there are pre-conceptual aspects to perception by any reasonable definition of conception. But without conceptual knowledge, people are "experientially blind."

R1.2. Mistaken similarities

Several commentators assumed that our psychological construction approach relies on Descartes' machine metaphor by inferring that psychological ingredients are encapsulated but interacting parts (see **de Gelder & Vandenbulcke**; **Pessoa**; **Vigil, Dukes, & Coulombe** [**Vigil et al.**]). Basic emotion models certainly use this metaphor in assuming that emotions work like mechanisms in a machine. Our model does not rely on traditional mechanistic models of the mind, however, and instead incorporates assumptions about constraint satisfaction (Barrett 2011a; Barrett et al. 2007d) (see Fig. R1). In constraint satisfaction, two or more processes have a nonlinear influence on one another, such that they exert mutual influence (Read et al. 1997) (but see Lewis [2005] for a basic emotion approach that utilizes similar concepts rather than a machine metaphor).[5]

A basic emotion approach usually ontologically reduces (i.e., redefines) emotions to their causes (brain locations or circuits) or parts (a behavior, e.g., **Jablonka & Ginsburg, Weisfeld & LaFreniere**). It is tempting to assume that psychological construction models also necessarily reduce emotions to their ingredients (**de Gelder & Vandenbulcke),** and indeed, some do (e.g., Duffy 1957; James 1884; Russell 2003). Our model, however, makes explicit use of the concept of emergence (see Barrett 2006b; 2011a; also see Wundt 1897), and so we explicitly assume that emotions cannot be merely redefined as their ingredients (cf. Gross & Barrett 2011). Instead, our model *causally* reduces emotions to neural firing (cf. Barrett et al. 2007d).

Furthermore, in our model, psychological ingredients are descriptions of what brain networks are doing at a psychological level as they combine to produce emergent mental phenomena (such as instances of *anger, memory, beliefs*, etc.; see Figure R2). The concept of "psychological primitive" might be useful to describe a basic level of psychological operation (e.g., conceptualization) without reducing it to something biological (e.g., functional connectivity between midline cortical areas). As time goes on, research will reveal whether these psychological descriptions are "primitive" or whether something even more psychologically basic is needed.

R1.3. Other theoretical approaches

Commentators **Scherer** and **Sander** argue that we had left out the *appraisal approach* to understanding the nature and function of emotion. As we noted in our target article, we did not include a discussion of appraisal models because they typically do not contain targeted hypotheses about whether emotions are generated in specific locations, anatomically defined circuits, or domain-general interacting networks. Furthermore, we did not include appraisal approaches in Table R1 because these models come in two definable varieties (causal and constitutive appraisal models; discussed in Barrett et al. 2007c) that make it difficult to assimilate into a single theoretical approach. Causal variants assume appraisals have the power to coordinate and synchronize all aspects of an emotional response (Grandjean & Scherer 2008; Scherer 2009a; and Scherer's commentary here) and are therefore more similar to basic emotion approaches. Constitutive models treat appraisals as descriptions of experience during emotional episodes and are much closer

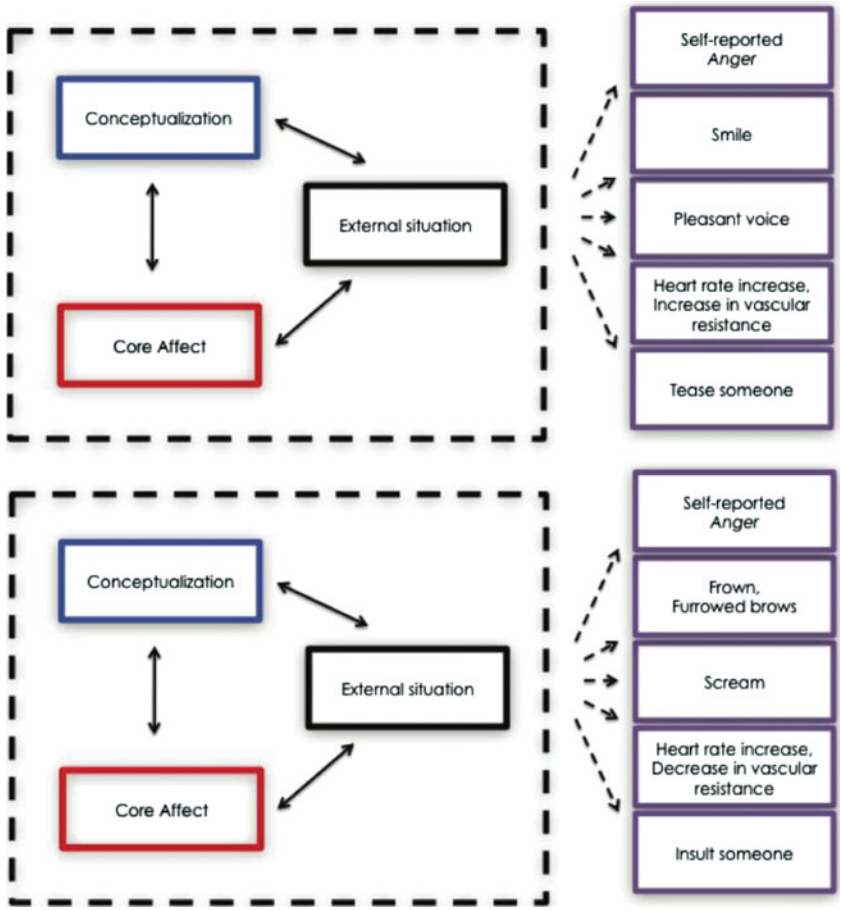

Figure R1. Our psychological constructionist model posits that core affect (red), sensory input from the world (black), and conceptual knowledge (including language – blue) mutually constrain one another to produce an emergent state that can be measured as a discrete emotion (purple). In a given instance of emotion (e.g., anger), the constellation of measures will take one pattern, and in another instance, it take a different pattern. A color version of this image can be viewed in the online version of this target article at: http://www.journals.cambridge.org/bbs.

to psychological construction accounts (e.g., Clore & Ortony 2000; 2008) (cf. Gross & Barrett 2011).

Our psychological construction approach can also be differentiated from other models in the emotion literature with which it shares a passing resemblance. In response to **Vigil et al.**, we point out that our psychological construction view (which relies on the idea of embodied, situated conceptualization) is distinct from other embodied

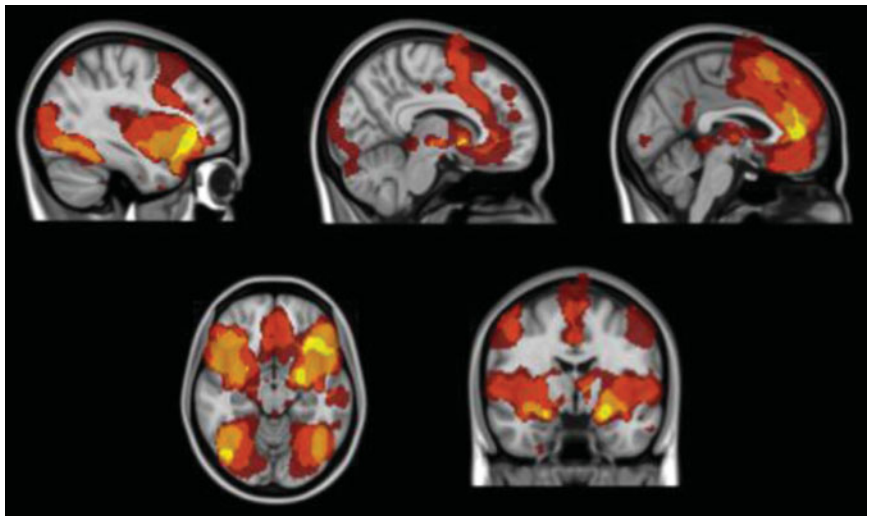

Figure R2. Intrinsic networks derived from resting state functional connectivity analyses that used peaks from Vytal and Hamann's (2010) meta-analytic anger, disgust, fear, and sadness contrasts as seeds. Yellow indicates that 4/4 networks overlap spatially in that area. Light orange indicates spatial overlap for 3/4 networks. Orange indicates spatial overlap for 2/4 networks. Red indicates no spatial overlap. A color version of this image can be viewed at http://www.journals.cambridge.org/bbs.

simulation models (e.g., Damasio 2000; Niedenthal 2007) that assume emotions are biologically basic categories with distinct somatic markers. In response to **Quirin & Lane**, we note that our model is also distinct from Lane's cognitive-developmental model of emotional awareness (Lane & Schwartz 1987) in which language is used to systematically differentiate global affective responses (for a more detailed discussion, see Lindquist & Barrett 2008b).

R2. The empirical status of the basic emotion approach

Having clarified these theoretical points, we now address commentaries that focus on the empirical status of the basic emotion approach. Several commentators have suggested that emotion categories can indeed be localized to specific brain locations, but that evidence to this effect was obscured by weaknesses in fMRI techniques, problems with our meta-analytic approach, or other variables. Others argue that evidence for basic emotion is best observed in responses other than those occurring in the brain. In this section, we address both types of issues.

R2.1. Emotions can be localized to specific brain locations

R2.1.1. Emotions might be localized to brain locations were it not for problems with the temporal resolution of fMRI. Several commentators raise the question of whether fMRI methods provide a suitable test of the brain basis of emotion, because they have poor temporal resolution. We agree that finer temporal resolution would be advantageous in studying the psychological functions of the brain, although we point to brain stimulation studies that also fail to find evidence that emotions can be localized to particular brain locations (sect. R2.3.4). These commentaries raise a deeper issue, however: writers hold beliefs about the timing of emotion that are a matter of definition and cannot be empirically tested. The suitability of fMRI for studying emotion comes down to how one defines emotion in the first place.

One underlying premise in some commentaries is that emotions are quick events that cannot be captured by fMRI's poor temporal resolution and the limits of a slow hemodynamic response (**Unoka, Berán, & Pléh** [**Unoka et al.**]; **Vigil et al.**; **Weisfeld & LaFrenier**). The concern is that "emotion centers" trigger very quickly after encountering a stimulus and regulatory brain areas fire only after emotion centers. If this were the case, then the Blood Oxygen Level-Dependent (BOLD) response might be too slow to capture emotion generation and regulation as separate events. Both production and regulation would be mistakenly included in the same contrast map, leading to the wrong conclusion about the nature of emotion. Unfortunately, it is not possible to empirically test how short an emotion is, but logically, it might not make sense to define emotion as a brief, exclusively feedforward event. Consider, for example, that almost instantly after a visual stimulus is presented, there is dynamic feedback and re-entrant processing between cortical and subcortical regions (Duncan & Barrett 2007; Lamme & Roelfsema 2000; Pessoa & Adolphs 2010; but see, de Gelder et al. 2011) that make it impractical to separate purely bottom-up and top-down influences in vision. Similarly, it might not make sense to try and separate an initial response from regulatory processes in emotion, as these distinctions might be more subjective and based on when they occur in time relative to stimulus onset, rather than on mechanistic differences (cf. Gross & Barrett 2011).

By contrast, other commentators (**Waugh & Schirillo**) believe that fMRI is problematic because emotions are episodes that evolve over time, and fMRI only captures the first second of neural response after stimulus onset. Timing is admittedly an important source of information. Yet, as reported in Waugh et al. (2010), the differences between the findings from their time-sensitive inverse logit modeling and the traditional (gamma) hemodynamic response function (HRF) modeling were not substantial enough to invalidate the studies summarized in our meta-analysis, meaning that it is possible to learn something about emotion from standard BOLD analyses. It is always possible that unmeasured variables such as time will more clearly differentiate emotion categories from one another, but the burden of proof is on those who wish to find such effects (i.e., the basic emotion view is not the null hypothesis).

A related concern was raised by **Vigil et al**., who are skeptical that changes in BOLD signal can be used to map the dynamics of neural activation. This is not a new point in the debate on whether neuroimaging can contribute to an understanding of the human mind. Although active investigation is ongoing and necessary, BOLD signals during fMRI do, in fact, match measures of integrated synaptic activity in the vast majority of cases, as evidenced by both direct studies (e.g., Logothetis et al. 2001) and convergence between animal studies and human meta-analyses across many fields (see Van Snellenberg & Wager 2009). Furthermore, every research technique has some kind of limitation. Electrophysiology is suspect because it does not measure or model neurochemistry. Neurochemical measurements do not consider electrical activity in detail. Lesion studies provide limited information about normative function. All nonhuman animal studies are limited because their subjects do not have human brains, which differ substantially in structure and connectivity (see Streider 2005). All human studies are limited because the available measurements are coarse and the potential for direct brain manipulation is limited. Neuroimaging data are thus useful to the extent that they converge with other methods and/or provide information of practical value, and in this regard, our meta-analysis provides one useful source of information. It is notable that our meta-analytic findings are consistent with meta-analyses and summaries of research in other measurement domains (in the face and body) that also fail to find strong support for the hypothesis that emotion categories are natural kinds (e.g., Bachorowski & Owren 1995; Barrett 2006b; Barrett et al. 2007a; Barrett et al. 2011; Cacioppo et al. 2000; Ortony & Turner 1990; Mauss & Robinson 2009; Russell et al. 2003), while at the same time being broadly consistent with a psychological construction approach to emotion (see sect. R3).

R2.1.2. fMRI does not have the spatial resolution to identify brain locations for emotion. Several commentators believe that fMRI has insufficient spatial resolution

to reveal emotion locations in the brain, on the assumption that emotion circuits reside in subcortical nuclei (**Buck**; **Quirin & Lane**; **Weisfeld & LaFreniere**) that are difficult to image with normal levels of resolution. It is an empirical question whether imaging methods with better spatial precision could localize different emotion categories to changes in midbrain and brainstem nuclei or sets of nuclei, but several observations make us predict that such an outcome is unlikely. First, although subcortical neurons are necessary for certain behavioral adaptations (e.g., freezing, fleeing, fighting) in nonhuman animals, it is not clear that there is a one-to-one correspondence between these adaptations and emotion categories (see sect. R2.3.1.). Second, some subcortical structures that are important to emotion (e.g., lateral hypothalamus) have a more diffuse anatomical structure in the adult human brain than in an infant human or nonhuman animal brain (Saper 2012), making it difficult to find clear localization. Third, existing evidence is not consistent with the hypothesis that finer levels of spatial resolution reveal the brain localization for different emotion categories. For example, in single cell recordings within the rhesus monkey brain, neurons throughout the amygdala respond preferentially to the screams of other monkeys but also respond to coos (positive sounds) and sounds indicating aggression (Kuraoka & Nakamura 2007). Taken together, studies like this suggest that no matter the degree of spatial resolution, the brain very likely does not contain "anger" neurons or "fear" neurons.

Perhaps most importantly, the hypothesis that emotions are subcortically generated and merely regulated by the cortex is based on an outmoded view of brain evolution (for an extended discussion, see Barrett et al. 2007a). **Buck** is correct when he writes that our meta-analysis identifies many of the brain structures discussed by Papez (1937) and MacLean (1952). But like all models of brain organization that rely on a phylogenetic scale, MacLean's triune brain concept is not correct (Striedter 2005). Some of the changes in connectivity that occurred during human evolution (e.g., the long-range connections between the isocortex and subcortical and spinal cord autonomic nuclei described in An et al. 1998; Öngür & Price 2000) produce the kind of re-entrant processing that is more consistent with a psychological construction account.

R2.1.3. Pairwise comparisons within our meta-analysis would have revealed evidence for emotion localizations. Commentator **Hamann** believes that we would have found better evidence for biologically basic emotion categories in our meta-analysis if we had performed pairwise comparisons between all categories. Vytal and Hamann (2010) performed these comparisons and found, as we did, that emotion categories were consistently but not specifically associated with increased activity in certain brain regions. For example, they report that both *anger*, when compared to *sadness*, and *disgust* when compared to *happiness*, were associated with increased activation in a region within the left inferior frontal gyrus (BA 47). Although the peaks themselves do not overlap, they are representative of broader clusters that do overlap. A similar point can be made for activity reported for the left insula, right insula, right basal ganglia, and amygdala in Vytal and Hamann's (2010) meta-analysis. Their findings, like ours, are therefore more consistent with our psychological construction approach that emotional experiences and perceptions are complex instances built from configurations of building blocks.

R2.1.4. Neural deactivations might help to identify brain locations for emotion. Commentators **Vigil et al.** argue that neural deactivations (which we did not include in our meta-analytic summaries) could potentially give evidence of cross-modal inhibition between brain areas that would reveal support for a locationist view of emotion. We agree that deactivations will contribute to a more complete picture of the brain basis of emotion, and we welcome further research that demonstrates their utility in meta-analytic summaries. One conceptual issue that must be addressed, however, is what the deactivations are relative to (i.e., whether there is really a baseline state of the brain; Stark & Squire 2001). "Rest," for example, means that the brain is not being probed by an external stimulus, but during "rest" a host of different mental processes are in play, including episodic memory retrieval and self-reflection (Andrews-Hanna et al. 2010).

On a more specific point, Vigil et al. misinterpreted our logistic regressions as showing that the amygdala was deactivated during *anger* perception. In fact, the logistic regressions indicated whether a variable was associated with an increase (positive beta) or decrease (negative beta) in activation frequency. Therefore, the finding that *anger* perception had a negative beta value means that it predicted a "0" for amygdala activation (versus predicting a "1"), meaning that *anger* perception was associated with less frequent activation of the left amygdala than other emotion categories on average.

R2.1.5. Evidence of emotion locations is obscured by less than perfect brain imaging studies that contribute to the meta-analytic summaries. Although we agree with **de Gelder & Vandenbulcke** on the "garbage in – garbage out" rule for meta-analysis, there are two major ways that the "meta-analytic whole" is greater than the sum of its parts (i.e., the individual studies). First, meta-analysis can weed out false positives (which are frequent in neuroimaging studies; see Wager et al. 2007; Yarkoni 2009) and focus interpretation on the activations that are consistently observed. Second, meta-analyses can provide a picture of whether the consistent activation is specific to one emotion category or another, which individual studies can rarely, if ever, do (i.e., it is rare to find studies that include five categories of experienced emotions).

R2.1.6. Individual differences might obscure evidence for brain locations for emotion. Commentators **Murphy, Ewbank, & Calder** [**Murphy et al.**] suggest that variation in person-level variables such as personality might impair researchers' ability to find consistent and specific increases in brain activity associated with discrete emotions. It is always a possibility that a third, un-modeled variable is adding more noise to signal, thereby preventing researchers from finding an effect. Still, according to a basic emotion view, the mechanisms and experiences of emotion are supposed to be universal (Ekman 1972; 1992; Ekman & Cordaro 2011; Izard 2011). The idea that personality produces variation in emotional

experience and perception is more consistent with a psychological construction approach. For example, almost two decades ago, our lab documented individual differences in the specificity with which people use emotion words to describe experience (termed "emotional granularity"; Barrett 1998; 2004; Feldman 1995) even though researchers often assume that *anger*, *disgust*, *sadness*, and other emotions are basic in a Roschian (1973) sense. For some people, however, *pleasant* and *unpleasant* appear to be more cognitively basic categories. For others, subordinate categories like *frustration* and *agitation*, and *depressed, morose, anxious terrified*, and so on, might be cognitively basic (Lindquist & Barrett 2008b). Although the neural responses realizing emotion might differ for people who differ in emotional granularity (an idea which has not yet been tested), the available evidence makes us skeptical that any of these categories are biologically basic and respected by the brain.

R2.1.7. Other "better" emotion categories might allow evidence of brain localization. Several commentators speculate on a variety of ways to classify emotion categories, premised on the assumption that there must be certain classes of emotions that will have special biological status: "animal/basic" versus "human/complex" emotions (**Jablonka & Ginsburg**; **Perlovsky**); "universal" versus "non-universal" emotions (**Weisfeld & LaFreniere**); "social" versus "non-social emotions" (**Jablonka & Ginsburg**); or "pure" versus "blended"/"mixed" emotions (**Scherer**). Weisfeld & LaFreniere further speculate that we chose to study the brain basis of *anger*, *disgust*, *fear*, *happiness*, and *sadness* because these are the categories with specific facial expressions. In fact, we chose these categories because amidst disagreement about which emotions are supposed to be biologically basic (Ortony & Turner 1990), most basic emotion researchers agree that these five are supposed to be inborn, universally experienced, and species-general (e.g., Ekman 1972; 1994b; Ekman & Cordaro 2011; Izard 1977; 2011). Thus, these emotion categories would be *most* likely to show strong localization if it exists.

Scarantino argues that *anger*, *disgust*, *fear*, *happiness*, and *sadness* categories are each too heterogeneous to yield evidence for locationism (in agreement with our psychological construction approach), and instead proposes that emotion researchers should refine each category into more homogenous subordinate categories (e.g., different types of *anger*) that would yield better evidence for locationism. Scarantino does not offer any concrete suggestions for how to identify these categories a priori, however. One promising possibility is that context plays an important role in characterizing meaningful subordinate categories (Barrett 2006a; Barrett et al. 2007b; Barrett et al. 2011). For example, a recent neuroimaging study from our group asked participants to construct a variety of experiences within two different emotion categories (*fear* vs. *anger*) across two different contexts (physical vs. social contexts). The neural representations for *fear* and *anger* largely overlapped, but there were distinctive neural responses for physical versus social instances (Wilson-Mendenhall et al. 2011). Context also seems to be important when searching for peripheral physiological correlates of emotion (Kreibig 2010). It thus may be fruitful to think of context itself as a sort of ingredient in emotion.

R2.1.8. Emotions can be localized to networks rather than gross anatomical regions. Once a 1:1 correspondence between gross anatomical regions and emotion categories is ruled out, a number of other possibilities for localizing emotions remain. For example, commentators **Hamann**, **Murphy et al.**, **Rothenberger**, **Scarantino**, and **Swain & Ho** all suggest that each emotion category is a natural kind if it is consistently associated with increased activity within a network of brain regions, rather than within a specific anatomically bounded set of voxels in one gross anatomical location. Indeed, the field of cognitive neuroscience has been moving steadily towards the conclusion that psychological functions are best described at the level of networks than at the level of individual brain regions. Our commentators do not consider the distinction, however, between a hard-wired, anatomical network and a dynamic functional network that is generated on the fly during an emotional experience or perception. This distinction is crucial for evaluating a basic emotion versus a psychological construction approach. It is tempting to claim evidence for basic emotions by merely showing that *any* pattern of brain activation distinguishes the instances of emotion category from another (e.g., as did Vytal & Hamann 2010); however, merely showing some difference is not sufficient support for the basic emotion view. A key hypothesis of the basic emotion approach is that emotions are innate, and this could mean that emotion networks, whether they are local or widely distributed, should be anatomically defined, intrinsic to the human brain, and present in other animals. A dynamic, functional network could be supportive of a weak version of basic emotions, but only to the extent that is consistently and specifically active during instances of a single emotion category.

One means of testing whether emotion categories can be localized to stable networks is to investigate "resting state" networks, which are evidenced as correlational patterns in low-frequency BOLD signal fluctuations across a set of voxels when participants are not being probed by an external stimulus. These data reveal a number of large-scale distributed networks that are anatomically constrained and intrinsic to the human brain (Buckner 2010; Deco et al. 2011; Fox & Raichle 2007; Vincent et al. 2007). A number of brain networks have been repeatedly identified and the task-related activity in these networks has been observed in tasks that involve attention, default mental activity, and motivational salience (Smith et al. 2009; Seeley et al. 2007; Vincent et al. 2007). Dozens of these studies have now been published, and no one has identified anything that remotely looks like basic emotion networks. Instead, emotion-related tasks appear to engage the "default" network (Andrews-Hanna et al. 2010) or what we have called the "conceptual" network. The degree of connectivity within a "body representation network" (with hubs in the ventral anterior insula and pregenual anterior cingulate cortex [ACC]) is correlated with individual differences in negative affect (Seeley et al. 2007) and the intensity of affective experience in response to negative images (Touroutoglou et al., in press). In a recent analysis, we took the peaks that were consistently activated for each emotion category

in Vytal and Hamann's (2010) meta-analysis and used them as seeds in a functional connectivity analysis of resting state data. Each seed/set of seeds produced an intrinsic network, but these networks largely overlapped for all the negative emotion categories (e.g., *anger, disgust, fear, sadness*); overlap was greatest in the ventral anterior insula, lateral orbitofrontal cortex, dorsal anterior cingulate cortex, and thalamus (Touroutoglou et al., in preparation; and see our Figure 2 on page 127). Rather than providing evidence for unique networks for basic emotions, these findings are consistent with our hypothesis about core affect.

R2.2. Localization is not required for the brain basis of natural kinds of emotion

Some commentators have criticized our characterization of the basic emotion view by arguing that such models do not require emotions to be localized to specific brain regions. Strictly speaking, they are correct – for an emotion category to be a natural kind, it must have firm boundaries in biology that exist independently of perception and there are two ways of fulfilling this criterion (Barrett 2006a; Barrett et al. 2007a). First, all instances of a category must be caused by the same biological mechanism (i.e., they must be homologous) or second, all instances must share a distinctive marker or collection of properties (i.e., they must be analogous). When testing for analogy, it is crucial that the measurements are objective and independent from a perceiver (e.g., facial electromyographic measurements are preferable to judgments of facial action; electrical changes in muscular or autonomic systems are preferable to judgments of behavior). Many writers define emotions as "basic" based on some version of both homology and analogy (e.g., Allport 1924; McDougall 1908/1926; Panksepp 1998; Tomkins 1962; 1963; Tracy et al. 2010), whereas some focus on homology (Ekman & Cordaro 2011; Griffiths 1997; Izard 2011) and others focus on analogy (e.g., **Buck**; Levenson 1994; 2003; Lewis 2005; Roseman 2011). Our meta-analytic findings, along with our review of the brain stimulation literature (Barrett et al. 2007a), do not support the hypothesis that emotion categories are natural kinds by homology. Many more empirical reviews demonstrate that emotions cannot be considered natural kinds by analogy (in chronological order: James 1890/1998; Duffy 1934; Hunt 1941; Mandler 1975; Ortony & Turner 1990; Turner & Ortony 1992; Cacioppo et al. 2000; Russell 2003; Barrett 2006a; Barrett et al. 2007a; Kagan 2007; Mauss & Robinson 2009). Although several individual studies report that emotion categories can be distinguished by different responses, many other studies do not support such claims, usually because no differences are found beyond valence and/or arousal (Barrett 2006a). Even the studies that do find differences fail to produce evidence that emotions are natural kinds by analogy, because the precise pattern of differences does not replicate from study to study.

R2.2.1. The production of facial actions will reveal natural kinds of emotion. Commentators **Caruana & Gallese**, **de Gelder & Vandenbulcke**, and **Vigil et al.** all write that each emotion category has its own universal expression. This is a deeply held belief in psychology, but for many years now there is evidence to the contrary. Congenitally blind infants (Fraiberg 1977) and children (Galati et al. 2001; Roch-Levecq 2006) who are not able to learn visually produce only a limited number of the predicted facial actions that are supposed to occur in prototypic emotional expressions; they almost never produce an entire configuration of the predicted facial action units (but then again neither do sighted adults; Galati et al. 1997). Careful laboratory studies show that 4-month-olds do not produce specific facial displays for *anger*, *fear*, *disgust*, and *sadness* (e.g., Bennett et al. 2002; 2004; for a review, see Camras & Fatani 2008; Camras & Shutter 2010) although infant facial actions give evidence of valence and arousal (Dinehart et al. 2005). Even 11-month-old infants fail to produce the predicted facial actions in response to an emotional event (e.g., in contexts designed to elicit *anger* and *fear*) (Camras et al. 2007). Although some researchers continue to adhere to the hypothesis that expressions develop according to pre-programmed timetables of emotional development (e.g., LaFreniere 2000; 2010; Sroufe 1997; and **Weisfeld & LaFreniere** in their commentary), many developmentalists now adopt a more flexible functionalist or dynamical systems approach to emotional development (e.g., Bennett et al. 2002; 2004; Camras & Fatani 2008, Camras & Witherington 2005, Dickson et al. 1998; Saarni et al. 2006) that does not require emotions to be natural kinds.

The infant findings are consistent with emotion production findings showing that adults do not routinely produce specific expressions in the laboratory when they are expected to (using objective measures of facial electromyography; Cacioppo et al. 2000). One hypothesis is that facial actions are thus symbols for communication rather than signals of the emoter's internal state (cf. Barrett 2011b; Fridlund 1994), because they occur largely when other people are present or implied (Fernandez-Dols & Ruiz-Belda 1995; Fridlund 1994). This research also echoes what has been observed with nonhuman animals. Nonhuman primates, for example, do not automatically produce vocal expressions unless they are in social contexts (Seyfarth & Cheney 2003). Of course, the field still awaits careful ethological study (beyond Eibl-Eibesfeldt's work) to explore whether humans actually make specific expressions in real-life instances of emotion.

R2.2.2. The perception of facial actions will reveal natural kinds of emotion. Commentators **Buck** and **Button, Lewis, & Munafò** [**Button et al.**] and **Smaldino & Schank** write that emotional expressions can be universally recognized, and this is often used as a criterion for showing that biologically basic emotions exist. Again, there is a considerable amount of research to the contrary. Studies that claim evidence for emotion perception in infants and children usually confuse affect (pleasant or unpleasant states with some degree of arousal) and discrete emotions (*anger*, *sadness*, *fear*, *disgust*, etc.). (Incidentally, a similar point can be made about research assessing event related potentials [ERPs] in response to emotional faces; see Barrett et al. 2007b for a discussion). For example, 5-month-old infants look longer at startled (or scowling, or pouting) faces after habituating to smiling faces (e.g., Bornstein & Arterberry 2003), but this increased looking time only gives evidence that

infants can distinguish between faces of different valence. Infants look longer at a pouting face after habituation to scowling faces (or vice versa) (e.g., Flom & Bahrick 2007), but this gives evidence that infants can categorize the faces in terms of arousal. Studies find that infants tend to show biased attention to *fearful* caricatures above other categories (e.g., Bornstein & Arterberry 2003), but this finding could be driven by the fact that infants rarely see people making these facial configurations. For example, infants look equally long at unusual facial configurations and fearful caricatures (DiCorcia & Urry, in preparation). Finally, it is important to rule out that infants perceive structural differences in faces without knowing what they mean. Seventeen-week-olds distinguish between faces showing teeth, whether those faces are from the same emotion category (e.g., both *happy* faces) or not (e.g., a *happy* and an *angry* face) (Caron et al. 1985). These findings with infants are consistent with the emotion perception findings with young children showing that children are unable to recognize emotion in faces until they have learned the associated emotion concept (for reviews, see Russell & Widen 2002; Widen & Russell 2008a; 2008b).

It is also not clear that nonhuman primates perceive discrete emotions. Claims have been made that nonhuman primates perceive discrete emotions based on findings from match-to-sample experiments in which animals select a face that matches a target face (i.e., perceptual matching). Chimpanzees are able to match a negative target face (e.g., "bared teeth") when the face stimuli choices includes one matching negative face (i.e., a "bared teeth") and one neutral face (Parr et al. 1998). Performance is inconsistent, however, when the stimuli choices are both negative faces (e.g., a "bared teeth face" with a "scream face"; Parr et al. 1998). Rhesus macaque monkeys also have the greatest success when they are able to differentiate between two stimuli choices based on affective (positive or negative) value. Macaques are able to correctly select the match for a positive face (i.e., "play face") on approximately 80% of trials when the two stimuli choices are a "play face" and either a neutral or a negative face (Parr & Heintz 2009). In contrast, matching accuracy of negative faces is extremely low (~50%) and inconsistent when the choices are other negative faces, the positive face ("play face"), or neutral faces (Parr & Heintz 2009). These findings suggest that nonhuman primates are readily able to distinguish faces that communicate affective signal from those that do not, but the data do not provide clear evidence that chimpanzees are categorizing faces in terms of their discrete emotional content.

Adults automatically perceive emotions on the face, but with a lot of conceptual input. Humans are "natural pattern classifiers" (to use **Smaldino & Schank**'s words) and we routinely include many sources of information as part of the patterns, including context and top-down conceptual knowledge (see Barrett et al. 2007b; 2011). For instance, studies showing that people from different cultures can universally recognize certain prototypic expressions (e.g., Ekman et al. 1987) have methodological features that produce high levels of emotion perception accuracy (Russell 1994). For example, the best results are achieved when perceivers are presented with a posed facial depiction of emotion (e.g., a scowling face) along with a list of between two and six emotion words, and then are asked to choose which word best matches the face. When emotion words are removed from the experiment or when perceivers are unable to process their meaning, people are significantly impaired in their ability to perceive emotion, even in faces that are supposed to be the clearest examples of emotional expressions (e.g., Fugate et al. 2010; Gendron et al., in press; Lindquist et al. 2006; Naab & Russell 2007; Roberson et al. 1999; Russell et al. 1993; for reviews, see Barrett et al. 2007b; 2011; Roberson et al. 2010; Russell 1994).

R2.2.3. Neurochemicals will reveal natural kinds of emotion. According to **Buck**, discrete emotional feelings arise from combinations or "cocktails" of neurochemicals. This is an interesting speculation, and provides an avenue for new hypothesis generation within a psychological construction approach. The difference between our view and Buck's view, however, is that he believes *anger*, *happiness*, *fear*, and so forth have special ontological status (Buck 1999) in that each correspond to the secretion of a particular pattern of neuropeptides. We know of no research to date that has systematically evaluated whether emotional experiences are linked to specific patterns of neurochemical secretion in a consistent and specific way, although there is evidence against Buck's assertion that specific neurochemicals correspond to "primary affects" (e.g., see Berridge & Robinson 1998; Horvitz 2000; 2002; Salamone et al. 2005; 2007; 2009; Schultz et al. 1993; Wise 2005; for a review, see Barrett et al. 2007a). As **Swain & Ho** suggest, future research should address the relationship between brain activity and hormone secretion.

R2.3. Other data that might reveal evidence for emotions as natural kinds

R2.3.1. Research using nonhuman animals provides evidence for natural kinds of emotion in the brain. Commentators **Jablonka & Ginsburg** present the idea that neural circuitry for behavior provides evidence for the brain basis of emotion. As we note in Table R1, this is a definition, based on assumptions about the continuity between humans and other animals, but it is not a testable hypothesis. Careful behavioral neuroscience research shows that there are specific neural circuits that control behavioral adaptations (highly heritable, species-general actions that an animal performs to survive or reproduce), but this work does not necessarily provide evidence to support the claim that emotion categories are natural kinds. For instance, years of careful study have confirmed that the amygdala plays a crucial role in several behavioral adaptations involved in responding to threat (e.g, freezing in response to a tone that was previously paired with an electric shock: Fanselow & Poulos 2005; Fendt & Fanselow 1999; LeDoux 2007; enhanced startle response as a function of a threatening or negative stimulus: e.g., Davis 1992). Yet, as we note in our target article, an animal can show many behavioral adaptations in response to a threat, and not all of them involve freezing or potentiated startle. Rats avoid the location of uncertain threat when they are free to move around, such as in a testing chamber with several arms (e.g., Vazdarjanova & McGaugh 1998). Rats will "defensively tread" by kicking bedding towards a threatening object (e.g., Kopchia et al. 1992; Reynolds & Berridge 2008). At other times, a rat will attack a threatening object by attempting to jump on it

and bite it (e.g., Blanchard et al. 1989). Each of these actions (freezing, potentiated startle, avoidance, defensive treading, and aggression) is dependent on different circuitry. Given this heterogeneity, it is difficult to claim that nonhuman animal research has identified the brain basis of *fear*, unless we are willing to assume that there are many *fear* circuits. Even then, how do we know for sure that defensive aggression is *fear* (rather than *anger*), or that freezing to an uncertain threat is *fear* (vs. *surprise*)?

R2.3.2. Brain activity during sleep reveals evidence of emotion locations in the brain. Commentators **Kirov, Brand, Kolev, & Yordanova** (**Kirov et al.**) claim that a psychological construction view of emotion is disconfirmed by the observation that people have increased activity in limbic regions during sleep and that they report emotions during dreams, even in the absence of activity in networks supporting executive attention. It is known that wakeful cognition can influence reports of dreams (e.g., people used to report dreaming in black and white before color television was invented), so one obvious issue in Kirov et al.'s logic is that people are awake when they report those experiences. Hence, the possibility remains that people add conceptual detail in retrospect while reporting on the strong affective feelings that were evoked during dreams. The deeper point is that situated conceptualizations do not require executive attention, as Kirov et al. presume; rather, controlled attention is required to suppress extraneous conceptual detail and keep the contents of emotional experience from being dysregulated from the situation (or disjointed and odd as often occurs in dreams). The fact that people dream (i.e., retrieve stored representations from the past and combine them in novel ways) is a testament to the fact that a dreaming brain is creating situated conceptualizations. Indeed, the brain regions making up the "default" network are active during sleep (although they appear to fire differently when a person is asleep than when awake; Horovitz et al. 2009). Finally, a key aspect of our psychological construction approach is that individual brain regions do not have a single psychological function; therefore, it is possible that, for example, the amygdala is not triggering emotion in sleep, or even processing novelty or salience per se, but instead is serving a function to produce and maintain REM sleep (e.g., Calvo et al. 1987; Sanford et al. 1995; Smith & Young 1980). Indeed, it is argued that limbic areas are involved in sleep because they are involved in consolidation of learned material (Maquet 2000), or perhaps even learned emotional material (Nishida et al. 2009) during REM periods.

R2.3.3. Clinical data might provide evidence of emotion locations in the brain. Although **Button et al., Murphy et al., Swain & Ho**, and **Rothenberger** all find value in our psychological construction approach, they each suggest that studies of clinical patients might provide evidence for the existence of biologically basic emotions. Although we agree that any account of the brain basis of emotion must include evidence from individuals who are suffering from disrupted emotional life due to psychopathology, there are a number of reasons to be skeptical that clinical data will reveal natural kind emotion categories when basic research does not. First, many psychiatric diagnostic categories have strong co-morbidity or share similar symptoms such as dysregulated affect, problems with conceptualization, of deficits in executive function. Second, many involve disturbances in the same brain regions. Third, and perhaps most importantly, many scientists recognize that current psychiatric diagnostic categories, like other complex psychological categories (e.g., *anger*, *sadness*, *fear*), are heterogeneous and the products of more general causes that might go awry (**Cramer, Kendler, & Borsboom** [**Cramer et al.**]). A paradigm shift is occurring in experimental psychopathology towards a transdiagnostic approach that attempts to identify the psychological and biological building blocks that are common to many types of psychopathology (e.g., Fairholme et al. 2010; Harvey et al. 2004; Kendler & Parnas 2008; Sanislow et al. 2010), and psychological construction accounts of mental illness are starting to appear (Kring 2008; Suvak & Barrett 2011).

R2.3.4. Deep brain stimulation or neuropsychological findings give evidence of emotion locations in the brain. Commentators **Caruana & Gallese**, **Staniloiu & Markowitsch**, **Hamman**, **Murphy et al.**, and **Weisfeld & LaFreniere** all point to the importance of brain stimulation and/or neuropsychological findings for evaluating the brain basis of emotion. Because of space limitations, we cannot report a comprehensive review of this literature, although we have reviewed it elsewhere (Barrett et al. 2007a). A careful look at the literature, however, indicates that the findings are more consistent with psychological construction than with locationism (in particular, see Halgren et al. 1978; Sem-Jacobson 1968; Valenstein 1974). For example, after their careful brain stimulation study, Halgren et al. (1978) concluded, "There is no apparent tendency for any category of mental phenomena to be evoked more easily from any particular site" (p. 97). More recent studies of brain stimulation provide similar conclusions (e.g., see Blomstedt et al. [2008] on the link between depression and stimulation of the subthalamic nucleus [STN], in combination with other studies showing that stimulation of the STN is not specific to depression [Bejjani et al. 1999; 2000; Doshi et al. 2002; Kulisevsky et al. 2002; Limousin et al. 1995; Romito et al. 2002]).

R3. The empirical status of the psychological construction approach

In this section, we discuss how scientific evidence supports the psychological construction approach, clarifying where its key hypotheses are supported by our meta-analytic findings and where future research is required.

R3.1. Utility of meta-analysis for testing psychological constructionism

Commentators **de Gelder & Vandenbulcke** raise the question of whether a meta-analysis of neuroimaging research is a useful way to evaluate the brain basis of emotion. They are concerned that methodological variation across individual studies might limit the degree of consistency that can be observed in meta-analytic summaries. Although this might be true, it is important to remember that we did find some consistency in the brain activations for each emotion category; the issue is that the activations were not specific to any emotion category. This pattern of

results (consistency with no specificity) is made more dramatic by the fact that most studies targeted the most typical instances of emotional experience and perception. Since context influences the neural representation of emotion (Wilson-Mendenhall et al. 2011), it is very likely that a reasonable sample of everyday instances of experience and perception would produce less consistent activations. Nonetheless, we agree with **Deshpande, Sathian, Hu, & Buckhalt** (**Deshpande et al.**) and **Pessoa** that psychological construction would be better tested using network-based approaches. Concepts and methods from neuroinformatics and systems neuroscience are a natural avenue for a psychological construction approach. Formal classification techniques, such as those used in statistical (or "machine") learning, could in principle be used to discover which kinds of psychological categories are most consistently and specifically respected in the brain (Mitchell et al. 2008; Yarkoni et al. 2011), potentially providing new tests of locationist versus constructionist approaches to emotion.

Hamann wonders whether our meta-analytic results provide sufficient evidence for a psychological construction approach to emotion, but of course no single analysis within a single measurement domain is ever sufficient. The fact that all methods have limitations makes it important to use multiple types of methods to test principled a priori hypotheses. We have tested our psychological constructionist view of emotion in our own laboratory by utilizing behavioral studies of normal adults (e.g., Fugate et al. 2010; Gendron et al., in press; Lindquist & Barrett 2008a; Lindquist et al. 2006; Lindquist et al., in preparation) and of lesion patients (e.g., Lindquist et al., under review), as well as individual neuroimaging studies (e.g., Wilson-Mendenhall et al. 2011). We look forward to a time when there are findings from more experiments to draw on.

Scherer wonders whether our meta-analytic results support an appraisal rather than a psychological construction model of emotion. He raises a series of theoretically deep questions about the nature of psychological causation and explanation. In Scherer's view, appraisals are psychological events (or checks) that are implemented by (or one might say, constructed by) domain-general mechanisms (such as executive function, categorization, minimizing prediction error, etc.). Since our hypothesis is that emotions are constructed from such mechanisms, this provides a valuable opportunity to explore the conceptual similarity between our two models. If appraisals describe what it is like to have a particular type of experience (i.e., are the "contents" of experience), as Scherer claims in his commentary, then there is very little difference in the predictions offered by our psychological construction view and his appraisal view, although Scherer would need to be clear about what his extra level of psychological description (i.e., the appraisals) contributes in terms of theoretical or predictive power. If appraisals, describe processes that cause emotions (i.e., are causal mechanisms) (see Grandjean & Scherer 2008; Sander et al. 2005; Scherer 2009a), however, then it is necessary to empirically evaluate which psychological descriptions are most effective – our ingredients or Scherer's appraisals.

R3.2. Other evidence consistent with psychological constructionism

We were excited to read that commentators found a psychological constructionist approach to be consistent with and generative for their own work. For example, **Jablonka & Ginsburg** discuss the important role of language in emotion, suggesting that language development and the ability to communicate emotions have contributed to humans' evolutionary success. **Quirin & Lane** also cite the importance of language in emotion, noting that in their view, language helps to differentiate a general, nonspecific affective response into complex, discrete emotional experiences. **Gardiner** points to fascinating research on emotional responses to music that are consistent with our psychological construction approach. **Staniloiu & Markowitsch** point out that psychological construction is consistent with neuropsychological and neuroimaging research on episodic-autobiographical memory, while a number of other commentators (**Cramer et al.**; **Humeny, Kelly, & Brook** [**Humeny et al.**]; **Rothenberger**; **Unoka et al.**) point to the similarities between psychological construction and a transdiagnostic approach to psychopathology.

Other commentators see our psychological ingredients as a useful avenue for understanding cross-cultural differences in emotion. Cross-cultural studies are important to our psychological constructionist model because they will help reveal whether core affect, conceptualization, executive attention, and language are universal psychological ingredients of the mind. For instance, **Unoka et al.** argue that there are clear cross-cultural differences in emotion knowledge that can shape how individuals from different cultures experience core affect. **Hechtman, Pornpattananangkul, & Chiao** (**Hechtman et al.**) suggest that the ingredients of core affect, conceptualization, and executive attention have the power to explain differences in brain activity observed among individuals of different cultures. One question that we find particularly interesting is whether there is cultural variation in certain emotion categories that might be basic in a cognitive (Rosch 1973) rather than in a biological sense. "Minimal universality" (cf. Russell 1995) might exist because many cultures were subject to similar selection pressures (e.g., living in large groups) and hence developed similar emotion concepts (Barrett 2006b). Other emotion concepts will differ cross-culturally. Even the same emotion categories can contain different content across cultures (e.g., *sadness* is an experience of physical agony in Russian but loss in English; Wierzbicka 2009; for reviews, see Mesquita & Frijda 1992; Mesquita & Walker 2003; Russell 1991; Wierzbicka 1992).

R4. Closing remarks

Our meta-analysis tested a simple version of faculty psychology: whether emotion categories map to consistent activations in specific locales of the brain. Our meta-analysis, along with some of the other research cited in our response, puts this view to rest. Although the meta-analysis was not optimized for testing a psychological construction view of emotion, its findings were largely consistent with this approach. Over time, the approach will continue to be refined, and understanding of the neural dynamics that create mental states will progress. For now, the psychological construction approach is useful because it dissolves old controversies, makes sense of persistent puzzles in the empirical literature (e.g., Barrett 2006a; 2009a), and

sometimes generates hypotheses that violate commonsense. For example, as **Scherer** correctly observes, the hypothesis that language is required for emotion experiences and perceptions means that animals, infants, or people without language would not experience or perceive discrete emotions (although we believe that they experience core affect) (see Lindquist et al. [under review] for an empirical example). Whereas Scherer sees this as a critique of our model, we view it as an interesting implication. In our view, the existence of emotion itself depends on the perceiver. To a human perceiver, who has a concept for *anger*, a growling dog is angry. From the dog's perspective, anger does not exist; a dog is engaging in a behavioral adaptation that is yoked to the specific context. But try telling a pet owner that his dog does not experience *anger* – it is like telling someone that the sky isn't really blue. Perceptions are powerful precisely because they usually mask the mechanisms that produce them.

NOTES

1. The roots of psychological constructionism date back to the beginning of psychology, however (see Gendron & Barrett 2009).

2. The exact nature of this bodily activation is sometimes described as raw somatic, visceral, vascular and motor cues (James 1884), arousal (Duffy 1957; Mandler 1975; 1990; Schachter & Singer 1962), or the mental representation of these cues as affect (Wundt 1897; Harlow & Stagner 1932; Hunt 1941) or core affect (Barrett 2006b; Barrett & Bliss-Moreau 2009; Russell 2003; Russell & Barrett 1999).

3. **Stapleton** wonders how bodily information and affect are related. Since the time of Wundt and James, psychologists and physiologists have been arguing about this very issue (for an empirical assessment of their relation, see Barrett et al. 2004; Wiens 2005). **Sander** wonders how affect can occur before the experience of novelty, but empirical evidence from our laboratory suggests that both affect and novelty are processed in the same neural circuitry, suggesting that they are not sequential properties of experience (e.g., Moriguchi et al. 2011; Weierich et al. 2010). The arousal regulated by the amygdala can be experienced as either affective feelings or novelty.

4. Candidates for meaning making include ideas (Wundt 1897), social affiliation (Schachter & Singer 1962), attribution (Russell 2003) or, as we propose in our model, conceptualization and categorization (Barrett 2006a; 2009b; Barrett et al. 2007a; 2007b; Lindquist & Barrett 2008a; 2008b).

5. Relatedly, the basic emotion approach usually assumes that emotions unfold in a linear fashion (an object triggers a dedicated brain location or circuit, which produces coordinated changes in behavior, peripheral physiology, and so on), and it is often assumed that psychological construction proposes a linear sequence as well (first a change in core affect, then this change is made meaningful by some additional process, like categorization). We do not propose any such linear sequencing, however. Although there are certainly instances where humans conceptualize core affect after the fact (i.e., disambiguating a feeling in the pit of the stomach as hunger vs. nervousness), there are also instances where category knowledge (primed by the situation) causes a shift in core affect. Most often, core affect and conceptualization are mutually constraining one another based on the situation (see Figure R1).

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[The letters "a" and "r" before author's initials stand for target article and response references, respectively]

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